THE UNIVERSITY OF ALBERTA

RELEASE FORM

NAME OF AUTHOR Lawrence D. Harder

TITLE OF THESIS Winter food habits of porcupines (*Erethizon dorsatum*) and their relationship to habitat use in montane forests of southwestern Alberta.

DEGREE FOR WHICH THIS THESIS WAS PRESENTED Master of Science

YEAR THIS DEGREE GRANTED 1977

THE UNIVERSITY OF ALBERTA

WINTER FOOD HABITS OF PORCUPINES (*ERETHIZON DORSATUM*) AND THEIR RELATIONSHIP TO HABITAT USE IN MONTANE FORESTS OF SOUTHWESTERN ALBERTA

by

© LAWRENCE D. HARDER

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

FALL, 1977

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend for acceptance, a thesis entitled "Winter food habits of porcupines (Erethizon dorsatum) and their relationship to habitat use in montane forests of southwestern Alberta" submitted by Lawrence D. Harder in partial fulfilment of the requirements for the degree of Master of Science.

ABSTRACT

The physical characteristics of conifers that had been fed upon by porcupines (*Erethizon dorsatum*) and of unused conifers were examined on two areas of montane forest in southwestern Alberta. The three vegetation types examined included a windward community co-dominated by limber pine and Douglas fir; a leeward forest of Douglas fir with scattered hybrid spruce; and a leeward community, also co-dominated by limber pine and Douglas fir, which appeared to be seral to the Douglas fir forest. The average age of conifers in these forests was approximately 65 years.

Of the factors considered, exposure and age were most influential in determining the size and form of trees measured on both areas, although density was also important in leeward forests. The superior growth rates of leeward trees relative to windward trees and the associated differences in phloem production probably account for the preference of porcupines for leeward trees. Although spruce grew more rapidly than Douglas fir and individuals of both species grew faster than windward limber pine, porcupines did not exhibit apparent interspecific preferences.

The trees used by porcupines commonly had extensive crowns and were larger and more vigorous than unused trees, so that they probably provided greater access to more abundant, better quality food. This type of tree was most frequent in low density stands of the leeward forests.

A greater proportion of the conifers on the Zoratti area were used by porcupines, even though trees on the Skelton area were more vigorous. This difference between areas appears to have been associated with the proximity of the Zoratti forests to summer feeding areas rather than differences in food or habitat quality. Because of the large number of porcupines using the Zoratti area, the average size of used trees was smaller than on the Skelton area. In addition, the pattern of repeated use of Douglas fir in the leeward pure forests differed between areas.

The use of both areas by porcupines peaked and declined in relation to the ages of the forests, suggesting that trees may become too large to be climbed and/or the declining growth rates of trees are associated with a reduction in the quality of inner bark. During winters of porcupine abundance, the use of poor quality stands increased. The nature of the observed preferences indicates some active selection of trees by porcupines. Although the actual mechanisms of tree selection are unknown, stand density and the physical characteristics of individual trees, particularly trunk diameter and crown size, are correlated with porcupine preferences. Winter food and habitat selection by porcupines in these areas appear to be interdependent.

ACKNOWLEDGEMENTS

I should like to acknowledge the support that I have received from the following individuals: V. Aziz, C. Henley, V. Loewen, R. McFetridge, D. Penner, and K. Smyth assisted in the field; Dr. B. Chernick, P. Pearlstone, and R. Weingardt helped to guide me through the data analysis; D. Moyles oversaw my initiation to manuscript production on the computer; and Dr. A. Bailey, Dr. W. Fuller, Dr. W. MacKay, and Dr. R. Nursall served on the supervisory and/or examining committees. I appreciate the generosity of Barney and Anne Zoratti and Bill and Mary Skelton in tolerating my activities on their lands.

Financial support for this project came from the National Research Council of Canada, as an operating grant to Dr. J. Murie and a Postgraduate Scholarship to myself, and the Department of Zoology at the University of Alberta, in the form of computing funds and a partial Graduate Teaching Assistantship.

Special thanks are due to Jan Murie and Dale Hensley for the blend of forbearance and concern that they have maintained towards my efforts. Without their help I would have jousted with many more windmills.

TABLE OF CONTENTS

LIST OF TABLES

Table		Page

INTRODUCTION

Environments are not homogeneous. If the relative ability of a habitat to provide food and protection, during both reproductive and fallow periods, is taken as a measure of habitat quality, those animals that can consistently detect and utilize the higher quality portions of their environment should make the greatest contribution to future generations. Variation in the value of food (net metabolizable nutrients) available within a particular habitat should increase the scope of selectivity that could be exercised by a given consumer to optimize fitness (Eadie 1970). Food selection should therefore be an integral part of the habitat utilization pattern of any mobile animal.

Porcupines (*Erethizon dorsatum*) are particularly good subjects for examining the association between food and habitat selection because evidence of their winter feeding is both obvious and long-lived. During the summer, porcupines feed on herbaceous vegetation and the foliage and catkins of some deciduous trees (Dodge 1967; Brander 1973). Concurrent with the cessation of plant growth and the onset of breeding in the fall, porcupines move to areas more heavily wooded than their summer ranges and begin to feed on the inner bark of woody plants and the foliage of several coniferous species (Gabrielson and Horn 1930; Curtis and Wilson 1953; Brander 1973). When feeding on inner bark, porcupines remove both the cambium and the phloem, exposing

the xylem. During subsequent growth periods this exposed xylem is slowly covered by the centripetal growth of callus tissue formed from the surrounding cambium (Brown 1971b). The resulting scars are a semi-permanent record of the amount and location of bark removed and of the year in which feeding occurred. Although barking may occur at ground level, especially in saplings, most feeding occurs within the crown of the tree (Taylor 1935). Since porcupines often use the same tree for food and shelter, winter food and habitat selection by this species may be intimately related.

The preferential use of a portion of a resource need not be a direct result of selective behaviour because the dispersion of a group of consumers may be controlled by the distribution of other essential resources (Wiens 1976). Porcupines could exhibit preferences at four successively finer subdivisions of a forest: forest types; stands within a type; individual trees; and portions of a tree. The quality of each of these subdivisions is dependent upon the quality of every other subdivision as well as the direct influences of the physical environment (Billings 1952), and it was the effect of these interrelationships on porcupine preferences which formed the focus of this study. Of particular interest were characteristics of feeding that were suggestive of active food or habitat selection.

Previous ecological studies of porcupines have been largely directed at the silvicultural significance of this species (Taylor 1935; Curtis 1941; Krefting _et al_. 1962;

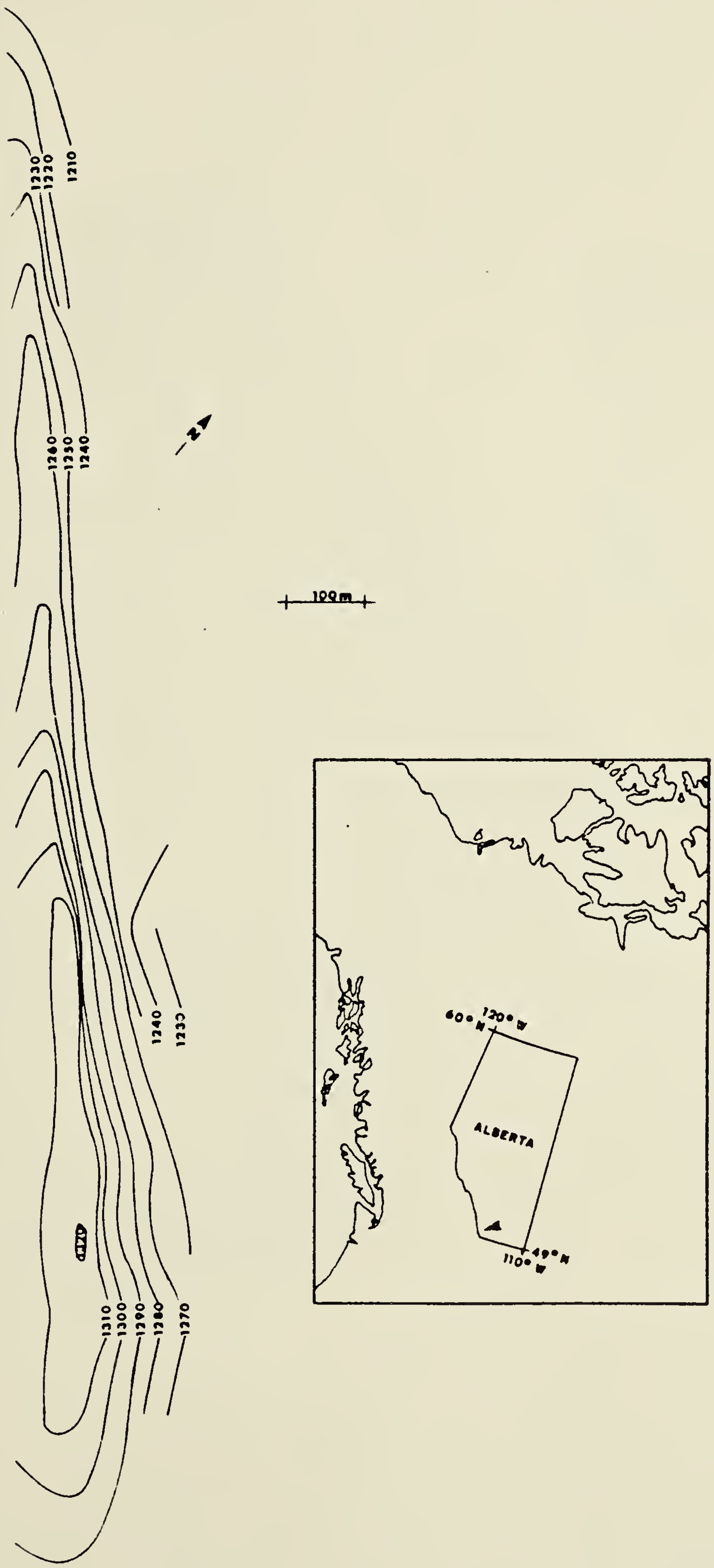
van Deusen and Myers 1962). Although these studies are the source of much of the information regarding porcupines, their ultimate interests were with the forest rather than with the animals. An alternative approach, which emphasized the dependence of porcupines on the nature of the forest, was adopted during this study.

STUDY AREAS

Two areas were intensively examined during the course of this study, both located on the eastern fringes of the foothills belt that runs along the base of the Front Ranges of the Rocky Mountains. The Zoratti study area (49°27' N; 114°04' W: Sec. 10, 15, 16 Tp. 6 R. 1 W. 5), located 11 km west of Pincher Creek, Alberta, covers an area of 36.3 ha and varies in elevation from 1210 to 1320 m (Figure 1). The Skelton study area (49°34' N; 114°13' W: Sec. 21, 22 Tp. 7 R. 2 W. 5), situated 16 km northwest of the Zoratti site, encompasses 115.4 ha and ranges in elevation from 1180 to 1360 m (Figure 2).

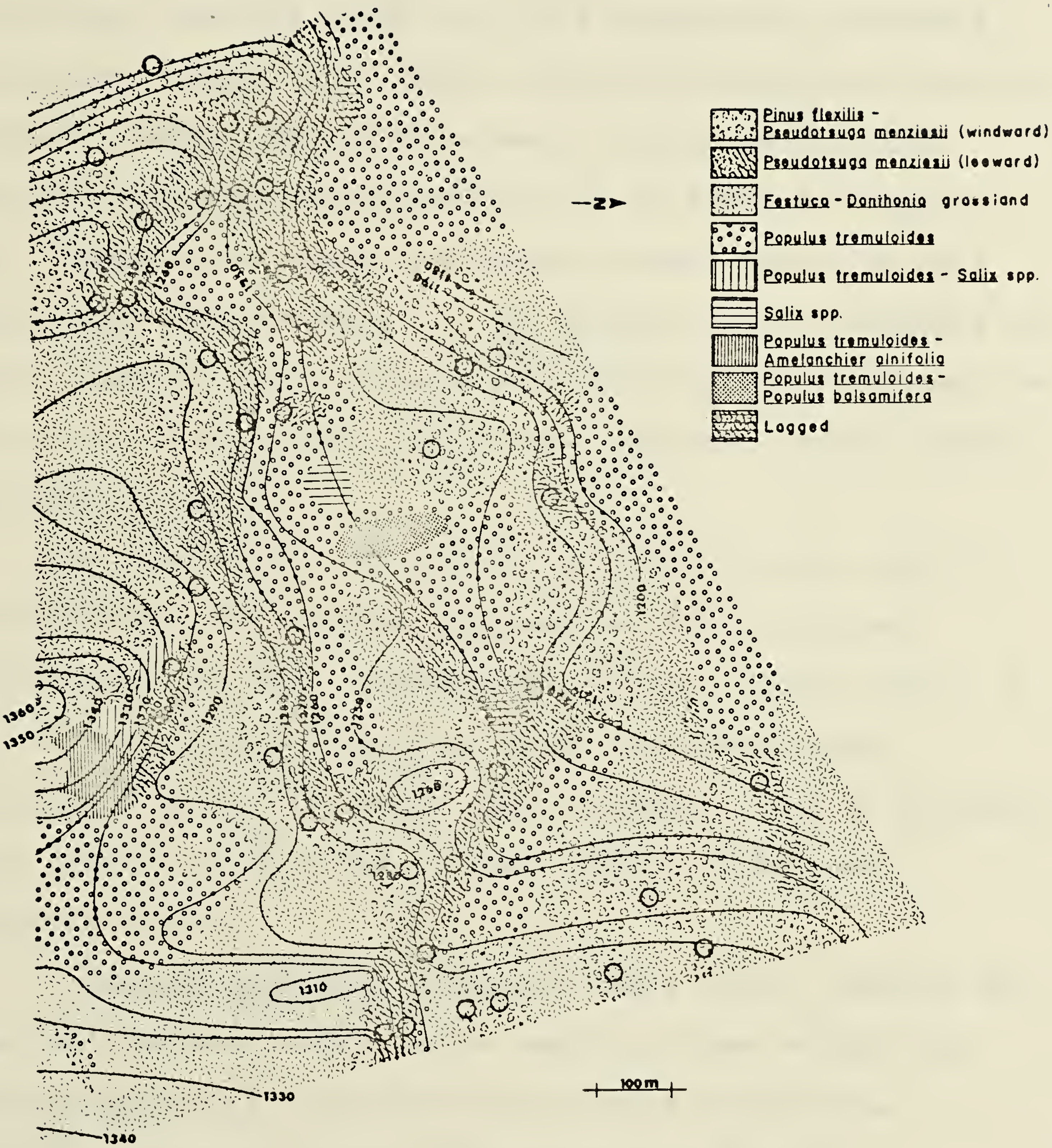
Parallel ridges of thrust-faulted and folded Cretaceous sandstones with a northwest-southeast orientation characterize the foothills of this region. Fault blocks in the area were thrust over adjacent blocks to the east so that west-facing slopes are gentler than those facing east. With the exception of portions of the ridgetops, the entire region is covered by a veneer of glacial till of varying thickness (Beaty 1975). Although both study areas were located on this system of ridges, exposure on the Skelton site was dominated by the valley of the Crowsnest River to the north. This valley was carved by an early-Pleistocene valley glacier which cut across the system of ridges, greatly altering local aspect (Beaty 1975).

Figure 1. Map of the Zoratti study area and its geographical location (inset). Contour interval 10 m.



1210
1220
1230
1240
1250
1260
1270
1280
1290
1300
1310
100m
60° N
120° W
ALBERTA
49° N
110° W

Figure 2. Map of the Skelton study area including the distribution of vegetation types and the locations of the sampling plots (open circles). Contour interval 10 m.



Pinus flexilis - Pseudotsuga menziesii (windward)
Pseudotsuga menziesii (leeward)
Festuca - Danthonia grassland
Populus tremuloides
Populus tremuloides - Salix spp.
Salix spp.
Populus tremuloides - Amelanchier alnifolia
Populus tremuloides - Populus balsamifera
Logged
N
100 m
1360
1350
1330
1340
1310
1200
1290

The proximity of this region to the Crowsnest Pass has a marked effect on its climate. Opening directly onto the plains, this pass serves as a channel for Pacific air flowing into Alberta (Longley 1972). As a result, prevailing westerly winds are often intense and seemingly omnipresent (Table 1). These winds often take the form of a Chinook (foehn), involving a warm, dry air mass, which greatly increases evapotranspiration in exposed locations. The Pincher Creek region can expect almost 300 cm of snow during the winter (Table 2), but because of the frequency of warm, westerly winds the exposed slopes of the foothills are bare much of the winter, while the sheltered leeward slopes are snow-covered.

The physiognomy and climate of the foothills west of Pincher Creek are together responsible for a distinct distribution of plant communities (Figure 3: Moss 1944). A brief description of the four major vegetation types recognized on the two study areas (Figures 2 and 4) follows; more detail can be found in Moss (1944) and Moss and Campbell (1947).

A *Festuca-Danthonia* community (Moss 1944), regarded by Moss and Campbell (1947) as an edaphic climax within the *Festuca scabrella* association maintained by moderate grazing, dominated south- and west-facing slopes.

An open, limber pine (*Pinus flexilis*)-Douglas fir (*Pseudotsuga menziesii* var. *glauca*) woodland occupied the ridgetops and the more windswept western exposures. The

Table 1. Percentage frequency and mean speed of winds from the most prevalent directions at Pincher Creek, Alberta, 1960-1972. (Information supplied by the Atmospheric Environment Service of Environment Canada.)

	Direction								
	SW		WSW		W		WNW		Calm
Month	%	km/hr	%	km/hr	%	km/hr	%	km/hr	%
January	4	19.5	15	36.5	37	35.5	6	20.0	15
February	4	18.4	18	34.6	40	33.0	5	18.1	14
March	6	18.7	20	29.9	33	28.3	5	16.0	14
April	7	19.7	23	30.4	30	27.7	5	14.9	12
May	7	18.2	13	26.1	30	24.2	6	14.9	12
June	7	16.6	22	26.2	29	22.7	7	16.2	14
July	9	16.6	18	22.6	28	21.1	7	15.0	16
August	9	17.4	18	23.5	31	21.3	7	14.1	15
September	8	17.3	20	25.6	31	23.8	6	15.4	15
October	6	19.0	24	31.4	41	30.1	6	18.2	10
November	5	19.0	21	31.4	40	31.4	6	19.8	13
December	4	20.0	16	33.8	41	32.6	7	20.5	15

Table 2. Temperature and precipitation means for the winter months at Pincher Creek, Alberta, 1960-1972. (Information supplied by the Atmospheric Environment Service of Environment Canada.)

	Temperature (°C)			Precipitation (cm)	
Month	Daily Maximum	Daily Minimum	Daily Mean	Total	Snow
October	12.9	0.6	6.8	2.79	25.1
November	4.8	-6.3	-0.7	2.59	30.0
December	-1.6	-12.2	-6.8	3.33	42.9
January	-3.9	-15.5	-9.7	3.89	52.3
February	2.2	-9.3	-3.6	2.44	32.0
March	3.9	-8.1	-2.1	3.28	41.9
April	9.8	-2.4	3.7	6.12	66.5

[illegible]

[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

Figure 3. A profile of the Zoratti study area, taken along the transect indicated by the opposing pointers in Figure 4, illustrating the relationship between slope and exposure and the distribution of vegetation.

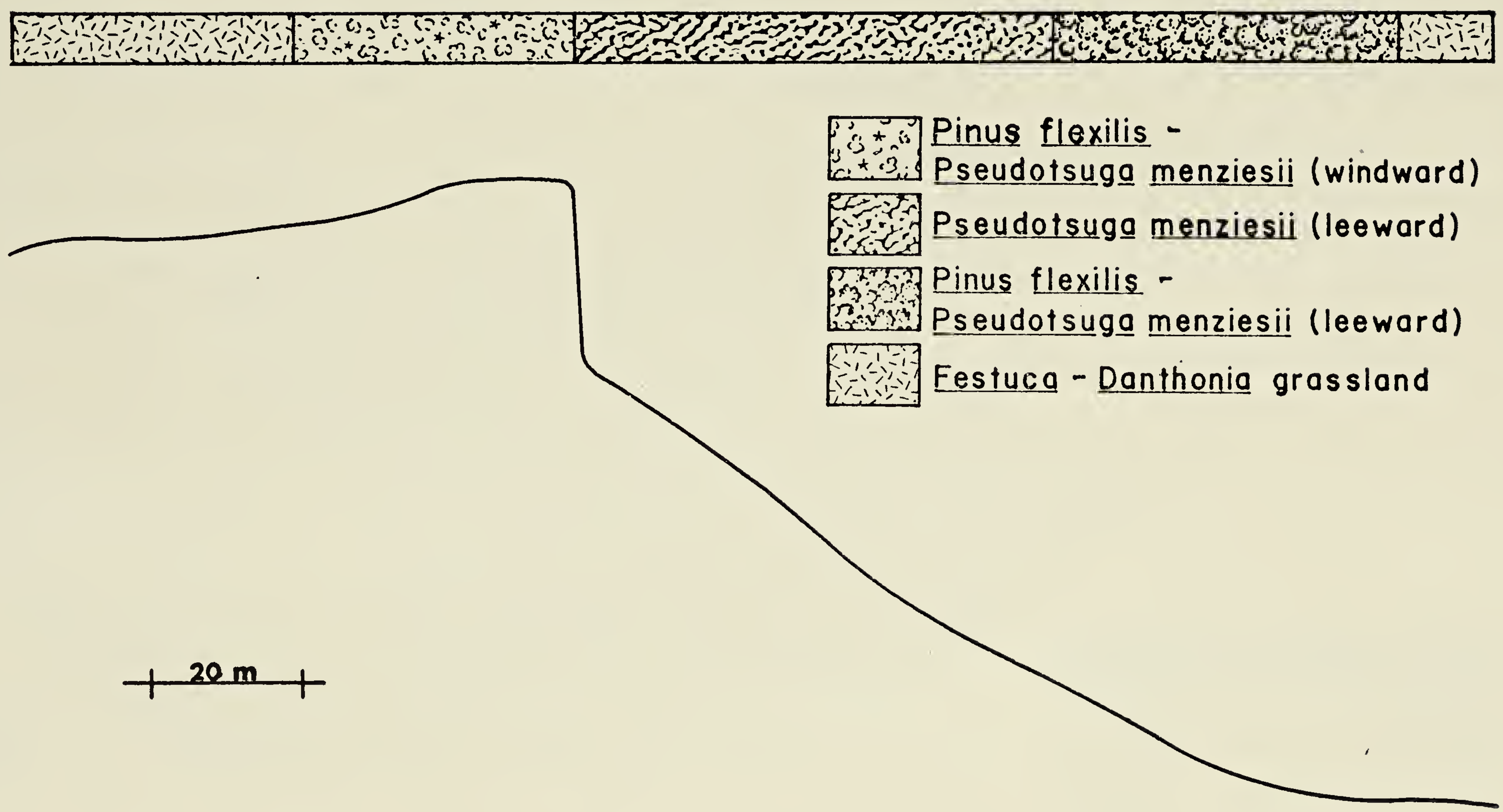
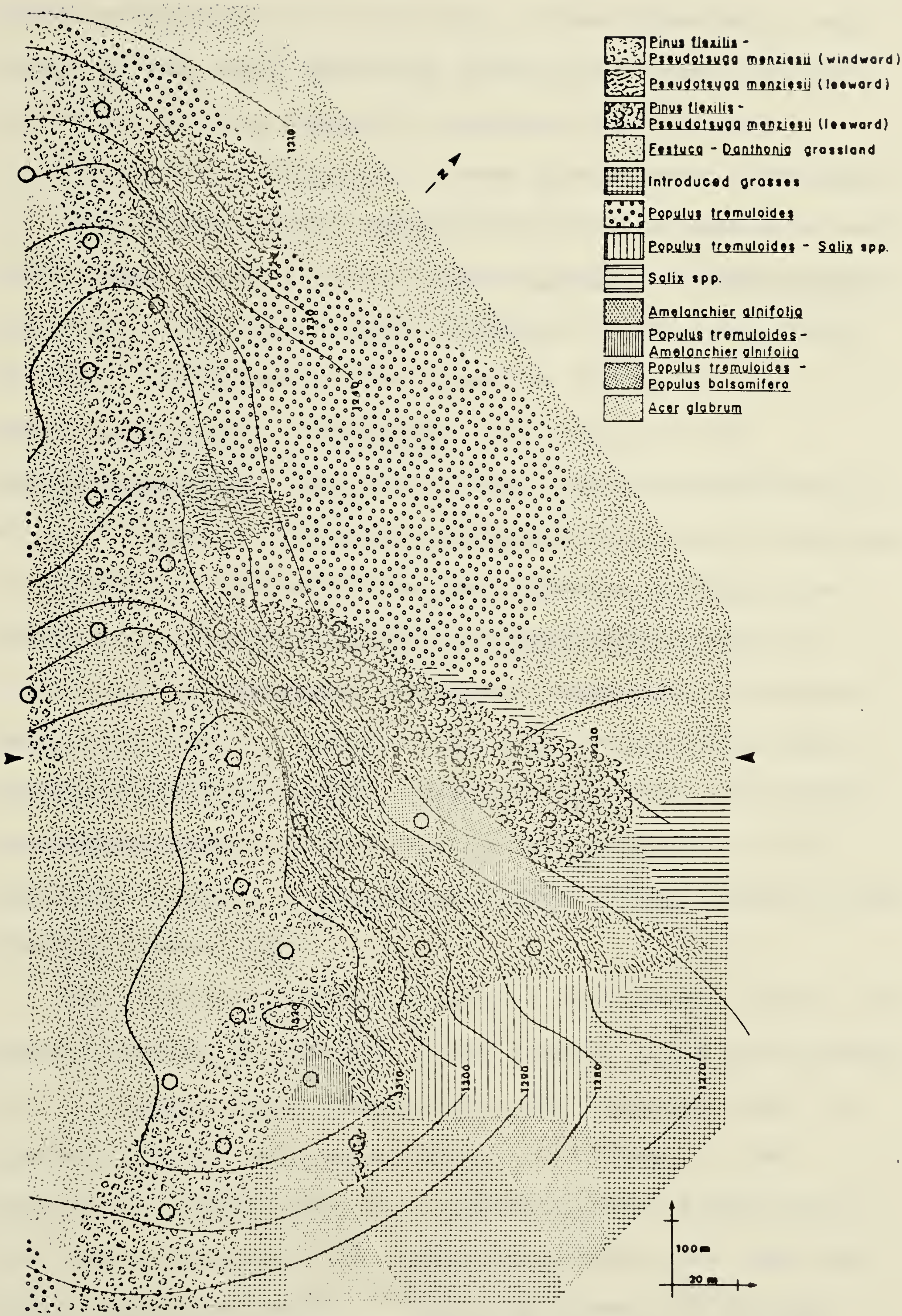

Pinus flexilis -
Pseudotsuga menziesii (windward)
Pseudotsuga menziesii (leeward)
Pinus flexilis -
Pseudotsuga menziesii (leeward)
Festuca - Danthonia grassland
20 m

Figure 4. Map of the Zoratti study area including the distribution of vegetation types and the locations of the sampling plots (open circles). The left-right axis has been expanded by a factor of five. Contour interval 10 m.



Pinus flexilis - Pseudotsuga menziesii (windward)
Pseudotsuga menziesii (leeward)
Pinus flexilis - Pseudotsuga menziesii (leeward)
Festuca - Danthonia grassland
Introduced grasses
Populus tremuloides
Populus tremuloides - Salix spp.
Salix spp.
Amelanchier alnifolia
Populus tremuloides - Amelanchier alnifolia
Populus tremuloides - Populus balsamifera
Acer glabrum
N
1210
1230
1240
1320
1310
1300
1290
1280
1270
1230
100 m
20 m

relative proportions of the two tree species varied with the degree of exposure and soil depth, limber pine being more common on the least sheltered sites with exposed bedrock. Most trees in this community exhibited the stunted, asymmetrical form typical of trees growing near timberline.

Douglas fir forest occupied the leeward slopes of both study areas. Hybrid spruce (Picea glauca x P. engelmannii; Daubenmire 1974) are a minor component of this community, and other coniferous species, such as lodgepole pine (Pinus contorta var. latifolia) and subalpine fir (Abies lasiocarpa), are rare. Rowe (1972) stated that the montane forest, of which this community is a part, developed in response to the prevailing dry climate, although the lower, and presumably eastern distributional limit of Douglas fir is influenced by summer moisture deficiencies (Daubenmire 1943). Areas to the west of the study sites receive more precipitation (Wyatt et al. 1939) and support extensive stands of hybrid spruce characteristic of the subalpine forest of the eastern slopes of the northern Rocky Mountains (Rowe 1972).

With decreasing slope along the base of the ridge, the leeward Douglas fir forest on the Zoratti study area graded into a younger limber pine-Douglas fir community that is apparently seral to a purer Douglas fir forest. The presence of limber pine as a pioneering tree species may have been a result of the isolation of this area from the western subalpine forest. The usual pioneer of eastern

slope forests is lodgepole pine (Cormack 1953), but only a single lodgepole pine was found on this study area.

Aspen poplar (Populus tremuloides) groves are located in flatter areas which are well drained and protected from the wind. As the quality of drainage declines, the aspen give way to balsam poplar (P. balsamifera) and then to willow (Salix spp.) and water birch (Betula occidentalis). Willows (S. bebbiana, S. scouleriana, and others) are the only local deciduous species that are used as winter food by porcupines.

Although a few fire-scarred trees exceeding 250 years of age are known from both study areas, the vast majority are less than 90 years old. Dawson (1886) reported large tracts of burned timber in the foothills of southern Alberta which he attributed to the initial use of the Crowsnest Pass by white travellers during the latter half of the nineteenth century. The forests on both study areas are probably the products of regeneration following extensive fires at that time.

METHODS

A total of 2561 trees were sampled on 20 x 20 m plots during the summers of 1974 (Zoratti) and 1975 (Skelton). The 38 plots examined on the Zoratti area (Figure 4) were regularly distributed along transects, separated by 100 m intervals, that traversed the ridge perpendicular to its long axis. Centers of adjacent plots on the same transect were 45 m apart so that 10 percent of the total area of the coniferous forests was sampled. A preliminary analysis of the data collected from these plots suggested that the intensity of porcupine use might have been related to stand density. To examine this relationship more rigorously, the 40 plots sampled on the Skelton area were chosen from 190 plots, distributed as on the Zoratti area, on the basis of the number of trees per plot and/or the uniformity of tree distribution (Figure 2). Several plots encompassing fewer than 20 trees were enlarged to cover an area of 500 sq. m. Stand density (number of trees/100 sq. m) was calculated as though each plot was level. Slope and exposure were measured for all plots using a compass and a Suunto clinometer.

Species, circumference at breast height (± 0.6 cm), height (± 0.3 m for trees under 7 m; ± 1.5 m for taller trees), and evidence and the probable cause of leader damage were determined for all trees taller than 1.35 m (breast height). A random selection of 20 percent of the trees

within each plot were aged using an increment borer and a 10x hand lens. Cores were extracted at stump height since the age differential between conspecific individuals in different communities would be less at that height than at breast height. Each tree was then climbed and inspected for porcupine feeding scars, and a record made of the intensity of use (four classes based on the total scar area) for the tree as a whole and separately for the lateral branches and the bole. In addition, the age of use was established and the height range and intensity of use for each age estimated. Use age was ascertained by removing a portion of the scar tissue surrounding the feeding area with a knife and counting the annual rings from the level of exposure by the porcupine to the most recent xylem surface. This technique was a modification of the procedure employed by Spencer (1964) to document porcupine population fluctuations over a 225 year period.

Although Douglas fir and limber pine were sufficiently abundant to be adequately sampled with plots, spruce were poorly represented on both study areas and were generally found in clumps within the pure fir forest. Since the relative preferences for these species were of interest, the leeward pure forest on the Zoratti area was systematically searched for spruce trees. One tree was randomly selected from every three encountered and examined in the same fashion as trees within the plots.

Several parameters, not measured directly, were calculated for each tree. Diameter at breast height (DBH ± 0.2 cm) was derived from the measured circumference. The ratio of the DBH to the height served as an index of growth form, based on the direct relationship between bole diameter and crown width (Mitchell 1969). This conformation index (CI), generally ranging from 0.75 to 3.00, was only useful for intraspecific comparisons because growth form varies between species.

Upon examination of the data collected during 1974, it became apparent that the measured diameter at breast height would only be indirectly related to the dimensions considered by porcupines during previous years. To circumvent this problem an attempt was made to determine the DBH and height of each tree for the preceding 20 years. Cores extracted during the ageing of trees on the Skelton study area were placed in plastic milkshake straws until they could be inspected in the laboratory. In addition, the thickness of the bark (± 0.025 mm), extracted at breast height with the increment borer, was measured using a pair of vernier calipers. Since the cores extracted on the Zoratti study area had been discarded, this area was revisited and cores collected from 165 trees randomly selected from the sample plots.

In the laboratory, the annual growth increment (± 5 x 10^{-4} mm) for the past 20 years of each core was measured with the aid of a micrometer eyepiece and a Wild

dissecting microscope (200x). This process was aided by cutting a flat surface, perpendicular to the long axis of the tracheids, with a scalpel and viewing the cores under reflected light. The length of each core, from the pith to its outer surface, was measured with vernier calipers.

Calculation of the DBH of any cored tree, x years prior to measurement, employed the following basic algorithm. The radius inside the bark during the year of interest (IRx) was taken as the product of the inside radius at the time of measurement ((DBH/2)-BARK) and the proportion of total length (TC) represented by the length of the growth increment x years previous ($TC-\sum_{n=1}^{n=x} In$, where In is the length of the growth increment for any given year, n). Therefore,

$$IRx=[(DBH/2)-BARK]\bullet((TC-\sum_{n=1}^{n=x} In)/TC) \quad (1)$$

and the DBH during that year was calculated using the linear regression equation relating the inside radius at the time of measurement to the measured DBH (Husch <u>et</u> <u>al</u>. 1972). The error associated with this regression equation is probably negligible since the smallest coefficient of determination (r^2) calculated was 0.997.

Since cores were extracted at stump height, a correction term was required to account for the shorter total core length at breast height. The age of a tree at breast height (ABH) was estimated using regression equations, of the form log(HT)=a+b(1/AGE) (Husch 1963), relating height and age for each species in each community. The length of the proximal portion of the increment cores

representing growth prior to this estimated age was then subtracted from the total core length providing an estimate of the appropriate core length (TC) for calculating past diameters. An examination of the error associated with TC is presented in Appendix 1.

Using these data for cored trees from each forest type, multiple regression equations describing the relationship between the calculated DBH and the age and measured DBH were computed for each of the 20 years preceding measurement. These equations were subsequently used to estimate the past diameters of uncored trees. Age was included in all 20 prediction equations only if it was a significant contributor to at least half of the series; otherwise the measured DBH was used as the sole predictor in all equations. The use of age in these equations required an estimate of age for each tree derived from the appropriate linear regression equation relating the age and DBH of cored trees.

The procedure applied in estimating the height of any tree, during the 20 years prior to measurement, utilized the relationship between height and DBH. Of the four general equations suggested by Husch _et al_. (1972), the power curve (log-log transformation) provided the best fit to the regression of the measured height on the measured DBH. The growth of any tree was therefore taken as a straight line, on a log-log plot, between the measured height and DBH and a height of 1.35 m and zero DBH, allowing the estimation of

the height corresponding to any previously established DBH. Each value in this calculation was increased by one to avoid the technical problem involved in determining the log of zero (Sokal and Rohlf 1969). If the height growth had been interrupted by a factor other than a porcupine killing the leader or if such porcupine damage occurred greater than twenty years before measurement, previous heights were not calculated. Had the leader been killed by porcupines within 20 years of the time of measurement, the growth since the use occurred was estimated using a regression line between the height of the top of the uppermost feeding scar and the calculated DBH for the year during which feeding occurred and the measured height and DBH.

Although errors in measuring tree and use age and yearly growth increment could have arisen by overlooking false and/or missing rings (McGinnies 1963), this type of error was probably insignificant. Douglas fir and limber pine are both considered excellent dendrochronological material, in part because of a high correlation between ring formation and the annual climatic cycle (Schulman 1956). Schulman examined Douglas fir from three southwestern Alberta sites and found the frequency of locally absent bole rings ranged from 0-1.1 percent of the total number of rings, depending upon the degree of moisture stress. He also stated that "... false annual rings are of rare occurence in the dendrochronologic species of the northern Rocky Mountains...." (pg. 19). The age of very old scars

located on senescent branches at the base of the crown was probably less accurately measured than tree age because these old branches often expend more energy in respiration than they fix through photosynthesis and xylem rings are produced irregularly (Reukema 1959).

A variety of statistical techniques was applied in describing and interpreting the relationships between measured variables and in data reduction. Most of these tests are in common usage and do not warrant detailed explanation. The multivariate techniques are, however, not as widely known and a brief description of their major features has been provided in Appendix 2. Discussion of the statistical procedures followed in examining specific problems generally precedes the presentation of the related results. The log likelihood ratio test (G) was used in preference to the chi-square test for the reasons outlined by Sokal and Rohlf (1969). A probability level of ≤ 0.05 was considered statistically significant for all tests.

Different parametric tests were used in the comparison of two means, depending upon the relative sizes of their respective variances as determined by an F-test (Sokal and Rohlf 1969). The statistic derived from two samples with homogeneous variances is based on a pooled variance estimate and is distributed as Student's t with $(n1 + n2 - 2)$ degrees of freedom. If the variances were heterogeneous the pooled variance estimate becomes meaningless and the test statistic is therefore calculated using separate variance estimates

and is approximately distributed as Student's t with

$$\left(\frac{[(S1^2/n1)+(S2^2/n2)]^2}{[(S1^2/n1)^2/(n1-1)]+[(S2^2/n2)^2/(n2-1)]} \text{ ; rounded to the nearest integer} \right)$$

degrees of freedom (Nie *et al.* 1975). As a result of these differences all references to these tests will include: the test statistic (t); the probability of a similar random difference; the type of variance estimate used (S=separate; P=pooled); and the appropriate degrees of freedom.

Calculating past tree dimensions and the subsequent statistical analysis would not have been possible without the facilities of the Department of Computing Services of the University of Alberta. The Statistical Package for the Social Sciences (Nie *et al.* 1975), supplemented by several APL programs, provided all of the statistical tests required. Problem-specific Fortran programs were used for data manipulation.

RESULTS AND DISCUSSION

Characteristics of Available Trees

If the physical size of a tree influenced its selection as a feeding tree by a porcupine, the attractiveness of a particular forest would be in part determined by the number of available trees with the preferred proportions. The appeal of this forest would be further influenced by the relative quality of adjacent forests, so that the factors affecting tree growth and distribution would indirectly affect the selection of food and habitat by porcupines. Since a tree's dimensions change with age, the appeal of a forest or tree could also be expected to change through time.

Although exposure was varied on the Skelton area, the open limber pine-Douglas fir forest (windward community) occurred predominantly on west-facing slopes while the closed canopy Douglas fir forest (leeward community) occupied more northern exposures (Table 3). Since the measured exposures for these two communities were symmetrically distributed around their respective means (mean, mode, and median vary by only three degrees for both communities), these mean exposures have been considered the optimum positions for each vegetation type. Only two exposures existed on the Zoratti area, neither of which approached these suggested optimum positions, so that the equivalent leeward forest (leeward pure) on the Zoratti area

Table 3. Exposure, slope, age, and species composition of the conifer dominated communities on the Zoratti and Skelton study areas. Each entry includes the mean, standard deviation and number of observations.

Forest Type		Exposure (degrees and direction)	Slope (degrees)	Age (years)	Species Composition (% Douglas fir)
Windward					
Zoratti	($\bar{X}$)	220.0 SW	12.5	67.0	16.5
	(s)	---	6.93	26.71	18.86
	(n)	18	18	137	11
Skelton		265.0 W	15.8	74.4	68.9
		35.00	9.30	19.31	34.79
		11	11	76	11
Leeward Pure					
Zoratti		40.0 NE	34.6	60.5	97.9
		---	5.59	19.31	4.10
		13	13	112	13
Skelton		357.1 N	20.1	66.5	98.6
		33.70	6.37	16.08	5.98
		29	29	246	29
Leeward Mixed					
Zoratti		40.0 NE	24.9	49.0	49.4
		---	5.08	18.77	26.80
		6	6	55	6
Combined					
Zoratti				61.6	
				23.70	
				304	
Skelton				68.4	
				17.19	
				322	

was restricted to the steeper slopes ($t=7.044$ $p<0.001$ P df=40) which receive less solar radiation. The younger ($t=3.657$ $p<0.001$ P df=165) mixed forest (leeward mixed) described earlier, is colonizing the gentler slopes ($t=3.575$ $0.01>p>0.001$ P df=16) on the leeside of the Zoratti area.

Dissimilar exposure and soil conditions were probably responsible for the differences between the windward communities on the two study areas. Limber pine was relatively more common on the Zoratti area ($t=4.391$ $p<0.001$ S df=15; Table 3) and a greater proportion of trees of both species in the Zoratti windward community exhibited the prostrate growth form characteristic of repeated moisture stress (Table 4: Brown 1971c). Exposure explained a significant proportion of the variation in the DBH (Table 5) of Douglas fir and the height (Table 6) of both species in the Skelton windward community. The more northerly exposed plots, although classed as windward on the basis of the associated herbaceous vegetation, contained trees of a form more typical of leeward plots.

Although aspect in part determines the intensity of insolation and the temperature and moisture content of both the soil and the atmosphere (Pearson 1920; McMinn 1952), it does not affect plants directly (Billings 1952). Tree species differ in their ability to deal with the available range of edaphic and atmospheric conditions so that exposure can be important in determining the distribution and local success of a species. Limber pine rely upon structural

Table 4. Proportion of prostrate trees in the windward communities on the Zoratti and Skelton areas.

	Study Area	
Species	Zoratti	Skelton
P. menziesii	29.3% (27/92)	1.8% (5/271)
P. flexilis	30.5% (163/535)	4.2% (5/117)

Table 5. Regression statistics describing the relationship between diameter at breast height and the measured environmental parameters. Additional statistics have been provided in Appendix 3.

	Independent Variables[1]	Beta[2]	R^2	Variables not in
P. menziesii				
Windward				
Zoratti {3}[3] (25)[4]	Age {4}	-0.740	0.548	Slope Density
Skelton {2} (54)	Age {4} Exposure {1} Density {4}	-0.583 0.553 0.276	0.542	Slope
Leeward Pure				
Zoratti {2} (104)	Age {3} Density	0.624 -0.374	0.633	Slope
Skelton {2} (247)	Age {3} Density {4}	0.699 0.288	0.570	Slope Exposure
Leeward Mixed				
Zoratti {3} (28)	Age {2}	0.823	0.677	Slope Density
P. flexilis				
Windward				
Zoratti {2} (94)	Age {2} Slope {4}	0.664 0.210	0.469	Density
Skelton {4} (19)	Age {4}	0.652	0.425	Slope Density Exposure
Leeward Mixed				
Zoratti (31)	Age	0.678	0.459	Slope Density

[1] $p<0.001$ for all equations except Skelton windward pine $0.005>p>0.001$.
[2] Beta (standardized regression coefficient) is a measure of the average effect that a change of one standard deviation in the independent variable has upon the dependent variable (expressed in standard deviations).
[3] Numbers in braces refer to the type of transformation applied: {1} squared; {2} square root; {3} log; {4} inverse. Braces following the study area name indicate that the transformation was applied to the dependent variable.
[4] Sample size.

Table 6. Regression statistics describing the relationship between height and the measured environmental parameters. Additional statistics have been provided in Appendix 3.

	Independent Variables[1]	Beta	R^2	Variables not in
P. menziesii				
Windward				
Zoratti {3}[2] (24)[3]	Age {4}	-0.632	0.399	Density Slope
Skelton {2} (49)	Exposure {1} Age {2}	0.467 0.438	0.304	Slope Density
Leeward Pure				
Zoratti (88)	Age {3} Density	0.667 -0.277	0.596	Slope
Skelton[4] (219)	Age {3} Exposure {4}	0.701 -0.109	0.487	Density Slope
Leeward Mixed				
Zoratti {3} (25)	Age {3}	0.792	0.628	Slope Density
P. flexilis				
Windward				
Zoratti {3} (83)	Age {3} Slope {4}	0.566 0.255	0.356	Density
Skelton {3} (12)	Exposure {1}	0.720	0.519	Slope Density Age
Leeward Mixed				
Zoratti {2} (26)	Age {2} Slope {1}	0.878 -0.391	0.551	Density

[1] $p<0.001$ for all equations except Skelton windward pine $0.025>p>0.01$.
[2] Numbers in braces refer to the type of transformation applied: {1} squared; {2} square root; {3} log; {4} inverse. Braces following the study area name indicate that the transformation was applied to the dependent variable.
[3] Sample size.
[4] Height of Skelton fir pure is not normally distributed.

adaptations such as stomatal reduction, thickened epidermis, and clustered leaves for protection against water loss, but in so doing restrict their ability to make use of light in photosynthesis. Douglas fir and spruce have adopted an alternative strategy, reducing water loss through physiological adaptations which are not as effective in extreme conditions of wind and dryness, but enhance photosynthesis and, therefore, growth (Bates 1923). As a result, limber pine is at a competitive disadvantage on all but the more xeric sites which are often exposurally distinct from closed canopy Douglas fir-spruce forests (Pearson 1920; Bates 1923; Marr 1967).

Although increasing slope appears to have had a negative effect on the size and form of windward limber pine on the Zoratti area (Tables 5, 6, and 7), the factor responsible for variation was probably soil depth since the slope of the steepest plots was dominated by the inclination of the bedding planes of the exposed bedrock. Slope may have acted more directly on the height and form of limber pine in the leeward mixed forest. This community appears to be advancing slowly on to flatter ground at the base of the ridge. The proportion of limber pine increases with decreasing slope (Spearman's rho=-0.900 t=3.576 df=3 $0.05>p>0.01$) suggesting that the developing pine trees ameliorate the conditions of the lower slopes allowing the establishment of Douglas fir which eventually replace the pine. Reduced light conditions in the presence of the

Table 7. Regression statistics describing the relationship between conformation index and the measured environmental parameters. Additional statistics have been provided in Appendix 3.

	Independent Variables[1]	Beta	R^2	Variables not in
P. menziesii				
Windward				
Zoratti (24)[3]	Age {4}[2]	-0.674	0.573	Density
	Slope {4}	0.298		
Skelton {3} (49)	Density {1}	-0.417	0.260	Exposure
	Age {4}	-0.335		Slope
Leeward Pure				
Zoratti {2} (88)	Age {4}	-0.354	0.265	Slope
	Density {3}	-0.312		
Skelton {3} (219)	Age {4}	-0.565	0.431	Exposure
	Density {3}	-0.372		Slope
Leeward Mixed				
Zoratti {2} (25)	Age	0.829	0.687	Density
				Slope
P. flexilis				
Windward				
Zoratti (83)	Age {2}	0.670	0.459	Density
	Slope {1}	-0.200		
Skelton (12)	Density {4}	-0.585	0.343	Age
				Exposure
				Slope
Leeward Mixed				
Zoratti (26)	Age	0.951	0.647	
	Slope {1}	-0.490		
	Density {4}	0.338		

[1] $p<0.001$ for all equations except Skelton windward fir ($0.005>p>0.001$) and Skelton windward pine ($0.05>p>0.025$).
[2] Numbers in braces refer to the type of transformation applied: {1} squared; {2} square root; {3} log; {4} inverse. Braces following the study area name indicate that the transformation was applied to the dependent variable.
[3] Sample size.

faster growing Douglas fir could have caused limber pine on the steeper slopes to develop longer, relatively thinner stems (see Brown 1971c).

Variation in age accounted for a significant proportion of the intraspecific variation in the DBH (Table 5), height (Table 6), and form (Table 7) of conifers in the three vegetation types examined, with the exception of limber pine in the Skelton windward community. The initial attempt at demonstrating the expected correlation between the age and DBH of the Skelton windward pine was unsuccessful until three of the small sample of aged trees (21) were excluded from the analysis. These trees were probably growing at a slower than normal rate since two forked a short distance above ground level and the third had partially fallen over. The ineffectiveness of age in explaining variation in the height of Skelton pine presumably resulted from a small sample size (n=12), compounded by the pattern of primary growth of limber pine, which involves a loss of vigour by the original leader (Marr 1967) and production of a more spherical crown than is typical for conifers (see Assmann 1970, pg. 39).

Stand density was another important factor influencing the size (Tables 5 and 6) and form (Table 7) of trees in the leeward pure forests of both study areas. The inverse relationship between density and DBH and height is a well known phenomenon that serves as the basis for the silvicultural practice of thinning (Assmann 1970). Crowding

restricts the size of the crown (Mitchell 1969) and therefore reduces the supply of photosynthetic products required for the growth of new tissues (Brown 1971a and b).

The variation in age and density, which seemingly played an important role in determining the form of the trees available to porcupines, was probably a result of the pattern of forest regeneration following burning. Several limber pine and Douglas fir, in excess of 200 years of age, were present on both study areas. The densest stands in the leeward forests generally occurred to the east (downwind) of, and in close proximity to, these older trees, suggesting that stand density is related to the distance from a seed source. Trees in the windward community, especially limber pine, appeared to be relatively more successful in surviving fire, presumably having been protected by the sparse ground vegetation and the open nature of this community. Because of a more evenly distributed seed stock, this protection, however slight, may explain the generally greater age of the windward community (Zoratti $t=2.228$ $0.05>p>0.02$ S $df=243$; Skelton $t=3.246$ $0.01>p>0.001$ S $df=109$; Table 3). Apparently the Zoratti area was burned somewhat later than the Skelton area since its forests were appreciably younger ($t=4.209$ $p<0.001$ S $df=550$; Table 3).

At the time of measurement, most of the trees on the Skelton area were older and larger than those on the Zoratti area (Tables 8, 9, 10a and 11a). Within each study area, trees in the leeward forest were generally larger than

Table 8. Descriptive statistics of the age and size of individual trees including the mean, standard deviation, and number of trees examined.

		Age (yr)	DBH (cm)	Height (m)	CI
P. menziesii					
Windward					
Zoratti	($\bar{X}$)	59.5	8.4	3.7	2.03
	(s)	25.55	6.18	1.77	0.837
	(n)	26	67	65	65
Skelton		74.2	15.1	6.6	2.33
		18.36	7.49	2.93	0.692
		54	254	235	235
Leeward Pure					
Zoratti		60.5	17.1	9.4	1.67
		19.31	9.92	4.28	0.592
		112	378	296	296
Skelton		66.5	19.9	11.8	1.61
		16.08	10.47	4.25	0.541
		246	1218	1057	1057
Leeward Mixed					
Zoratti		47.4	11.4	5.4	1.74
		19.83	9.25	3.46	0.715
		27	67	62	62
P. flexilis					
Windward					
Zoratti		68.8	9.1	3.1	2.70
		26.78	6.12	1.27	1.042
		111	370	299	299
Skelton		74.9	12.6	4.3	2.91
		21.93	7.35	1.75	0.930
		22	112	96	96
Leeward Mixed					
Zoratti		50.6	11.5	4.8	2.12
		17.92	6.76	1.96	0.831
		28	94	75	75
Picea spp.					
Leeward Pure					
Zoratti		63.2	24.7	12.4	2.00
		15.47	11.26	4.3	0.641
		8	49	46	46

Table 9. Comparisons of the ages of conifers on the Zoratti and Skelton areas. Comparison of Douglas fir in the three Zoratti communities is presented in Table 13.

Comparison[1]	Mean (yr)	t	p	df	Type
ZWF	59.5	1.61	p>0.1	135	P
ZPW	68.8				
SWF	74.2	0.14	p>0.75	74	P
SWP	74.9				
ZWF	59.5	2.63	0.02>p>0.01	38	S
SWF	74.2				
ZWP	68.8	1.00	p>0.25	131	P
SWP	74.9				
ZPF	60.5	2.87	0.01>p>0.001	184	S
SPF	66.5				
ZPF	60.5	0.39	p>0.5	118	P
ZPS	63.2				
ZMF	47.4	0.64	p>0.5	53	P
ZMP	50.6				
SWF	74.2	3.08	0.01>p>0.001	298	P
SPF	66.5				
ZWP	68.8	4.28	p<0.001	61	S
ZMP	50.6				

[1]Comparison code:
First character Z-Zoratti S-Skelton
Second character W-Windward P-Leeward pure M-Leeward mixed
Third character F-Douglas fir P-Limber pine S-Spruce

Table 10. Comparisons of the diameter at breast height of trees on the Zoratti and Skelton study areas. Comparison of Douglas fir in the three Zoratti communities is presented in Table 13. The extreme right-hand column bears the following code for interpretation of the analyses of covariance:

1 - Similar growth rates throughout;

2 - Different initial growth rates;

3 - Different growth rates throughout,

  a) Difference in growth curves corrected by log-log transformation

  b) Interaction - the slopes of the individual growth curves are not equivalent.

	a) t-test Means (cm)	t	p	df and Type	Adjusted Means (cm)	b) Analysis of Covariance F[1]	p	Trans[2]	F[3]	p	df	
ZWF[4]	8.4				11.3						1	
		0.89	p>0.2	435 P		8.407	0.005>p>0.001	{3}	80.225	p<0.001		2
ZWP	9.1				7.4						134	
SWF	15.1				16.5						1	
		3.06	0.01>p>0.001	364 P		9.664	0.005>p>0.001	{4}	11.313	p<0.001		2
SWP	12.6				11.0						73	
ZWF	8.4				12.0						1	
		6.82	p<0.001	319 P		3.282	p>0.05	{4}	36.389	p<0.001		1
SWF	15.1				15.4						77	
ZWP	9.1											
		4.55	p<0.001	160 S	Heterogeneous variances							
SWP	12.6											
ZPF	17.1				18.0						1	
		4.61	p<0.001	1594 P		1.603	p>0.10	{2}	220.000	p<0.001		1
SPF	19.9				19.1						355	
ZPF	17.1				16.3						1	
		4.94	p<0.001	425 P		18.685	p<0.001	{3}	85.054	p<0.001		2
ZPS	24.7				23.1						128	
ZMF	11.4				9.5[5]						1	
		0.04	p>0.9	114 S		0.773	p>0.25	{3}	111.057	p<0.001		1
ZMP	11.5				8.3						52	
SWF	15.1											
		8.56	p<0.001	485 S	Hetergeneous variances							
SPF	19.9											
ZWP	9.1				8.0						1	
		3.29	p<0.001	462 P		57.051	p<0.001	{3}	62.027	p<0.001		2
ZMP	11.5				15.6						136	

[1]This F-test examines the equality of the adjusted means.
[2]Transformation of the covariate: {1} squared; {2} square root; {3} log; {4} inverse.
[3]This F-test examines the contribution of age in explaining variation in DBH.
[4]Explanation of this comparison code is provided in Table 9.
[5]The dependent variable has been log transformed to correct for mildly heterogeneous variances.

Table 11. Comparisons of the height of trees on the Zoratti and Skelton study areas. Comparison of Douglas fir in the three Zoratti communities is presented in Table 13. The extreme right-hand column bears the following code for interpretation of the analyses of covariance:

1 - Similar growth rates throughout;

2 - Different initial growth rates;

3 - Different growth rates throughout,

a) Difference in growth curves corrected by log-log transformation

b) Interaction - the slopes of the individual growth curves are not equivalent.

	a) t-test				b) Analysis of Covariance							
	Means (m)	t	p	df and Type	Adjusted Means (m)	F	p	Trans[1]	F	p	df	
ZWF[2]	3.7	2.67	0.01>p>0.001	79 S	Heterogeneous variances							
ZWP	3.1											
SWF	6.6	8.96	p<0.001	288 S	[3]							
SWP	4.3											
ZWF	3.7	10.00	p<0.001	171 S	4.1[4]	10.106	0.005>p>0.001	{3}	34.568	p<0.001	1	3a
SWF	6.6				5.9						71	
ZWP	3.1	7.19	p<0.001	131 S	[3]							
SWP	4.3											
ZPF	9.4	8.51	p<0.001	1351 P	10.5	9.379	0.005>p>0.001	{3}	315.191	p<0.001	1	2
SPF	11.8				11.7						308	
ZPF	9.4	4.35	p<0.001	340 P	9.6	22.222	p<0.001	{3}	108.157	p<0.001	1	2
ZPS	12.4				14.2						101	
ZMF	5.4	1.38	p>0.1	92 S	Heterogeneous variances							
ZMP	4.8											
SWF	6.6	22.56	p<0.001	481 S	Significant interaction[5]				7.099	0.01>p>0.005	1	3b
SPF	11.8										263	
ZWP	3.1	7.07	p<0.001	90 S	Heterogeneous variances							
ZMP	4.8											

[1] Transformation of the covariate: {1} squared; {2} square root; {3} log; {4} inverse.
[2] Explanation of this comparison code is provided in Table 9.
[3] This analysis was not performed because age did not account for a significant proportion of the variation in the height of Skelton limber pine (Table 6).
[4] The dependent variable has been log transformed to correct for mildly heterogeneous variances.
[5] The following F-value represents the significance test for interaction.

windward trees, even though the windward forests were older. Although fir tended to be larger than pine within the windward community, there was no significant difference in the average size of these two species in the leeward mixed forest. Finally, the spruce in the leeward pure forest on the Zoratti area were larger, though not older, than the surrounding Douglas fir.

Conformation of trees also varied between forest types and study areas (Tables 12a and 13). (Interspecific comparisons involving limber pine do not appear in Table 12 because of its unusual pattern of primary growth.) The crowns of windward trees and leeward trees in low density stands often extended to within a meter of the ground, whereas often only the upper third of leeward trees in dense stands was foliated. Windward trees had stout trunks, compared to leeward trees of similar height, probably because of the stimulatory effect of wind-induced sway on secondary growth (Jacobs 1954). The Douglas fir in the leeward pure forest on the Zoratti area had more extensive crowns on average than their counterparts on the Skelton area as a result of a higher mean density on the latter area (Zoratti weighted mean (± se) 12.18 ± 0.286 trees/100 sq. m (n=359); Skelton weighted mean (± se) 17.08 ± 0.163 trees/100 sq. m (n=1221); $t=5.61$ $p<0.001$ P $df=1578$).

The observed similarities and differences in the size and form of trees can be interpreted by three complementary

Table 12. Comparisons of the conformation index of trees on the Zoratti and Skelton study areas. Comparison of Douglas fir in the three Zoratti communities is presented in Table 13. The extreme right-hand column bears the following code for interpretation of the analyses of covariance:

1 - Similar growth rates throughout;

2 - Different initial growth rates;

3 - Different growth rates throughout,

a) Difference in growth curves corrected by log-log transformation

b) Interaction - the slopes of the individual growth curves are not equivalent.

	a) t-test				b) Analysis of Covariance							
	Means	t	p	df and Type	Adjusted Means	F	p	Trans[1]	F	p	df	
ZWF[2]	2.03											
		2.65	0.01>p>0.001	90 S	Heterogeneous variances							
SWF	2.33											
ZWP	2.70				[3]							
		1.75	p>0.05	394 P								
SWP	2.91											
ZPF	1.67											
		1.66	p>0.05	442 S	Heterogeneous variances							
SPF	1.61											
ZPF	1.67										1	
		3.41	p<0.001	340 P	Significant interaction*				5.422	0.025>p>0.01		3b
ZPS	2.00										100	
SWF	2.33				2.24[5]						1	
		14.89	p<0.001	300 S		75.308	p<0.001	{3}	80.440	p<0.001		3a
SPF	1.61				1.51						264	
ZWP	2.70				2.29[5]						1	
		5.10	p<0.001	138 S		0.529	p>0.25	{3}	73.029	p<0.001		1
ZMP	2.12				2.46						114	

[1] Transformation of the covariate: {1} squared; {2} square root; {3} log; {4} inverse.
[2] Explanation of this comparison code is provided in Table 9.
[3] This analysis was not performed because age did not account for a significant proportion of the variation in the conformation index of Skelton limber pine (Table 6).
* The following F-value represents the significance test for interaction.
[5] The dependent variable has been log transformed to correct for mildly heterogeneous variances.

Table 13. Comparisons of the age, diameter at breast height, height and conformation index of Douglas fir in the three conifer dominated communities on the Zoratti study area.

Age - One-way analysis of variance

$F=4.523$ $0.01>p>0.025$ 2 and 162 df

Mixed Windward Pure
47.4 59.5 60.5 (Student-Newman-Keuls test p=0.05)

log DBH

a) One-way analysis of variance

$F=31.790$ $p<0.001$ 2 and 509 df

Windward Mixed Pure
8.4 11.4 17.1 (Student-Newman-Keuls test p=0.05)

b) Analysis of covariance
covariate - log Age $F=177.281$ $p<0.001$

$F=11.457$ $p<0.001$ 2 and 161 df

Windward Pure Mixed (adjusted means)
6.6 12.3 13.2 (Student-Newman-Keuls test p=0.05)

log Height

a) One-way analysis of variance

$F=75.822$ $p<0.001$ 2 and 420 df

Windward Mixed Pure
3.7 5.4 9.4 (Student-Newman-Keuls test p=0.05)

b) Analysis of covariance
significant interaction

$F=9.607$ $p<0.001$ 2 and 136 df

CI - Heterogeneous variances

a) Approximate F-test (Sokal and Rohlf 1969: 376-379)

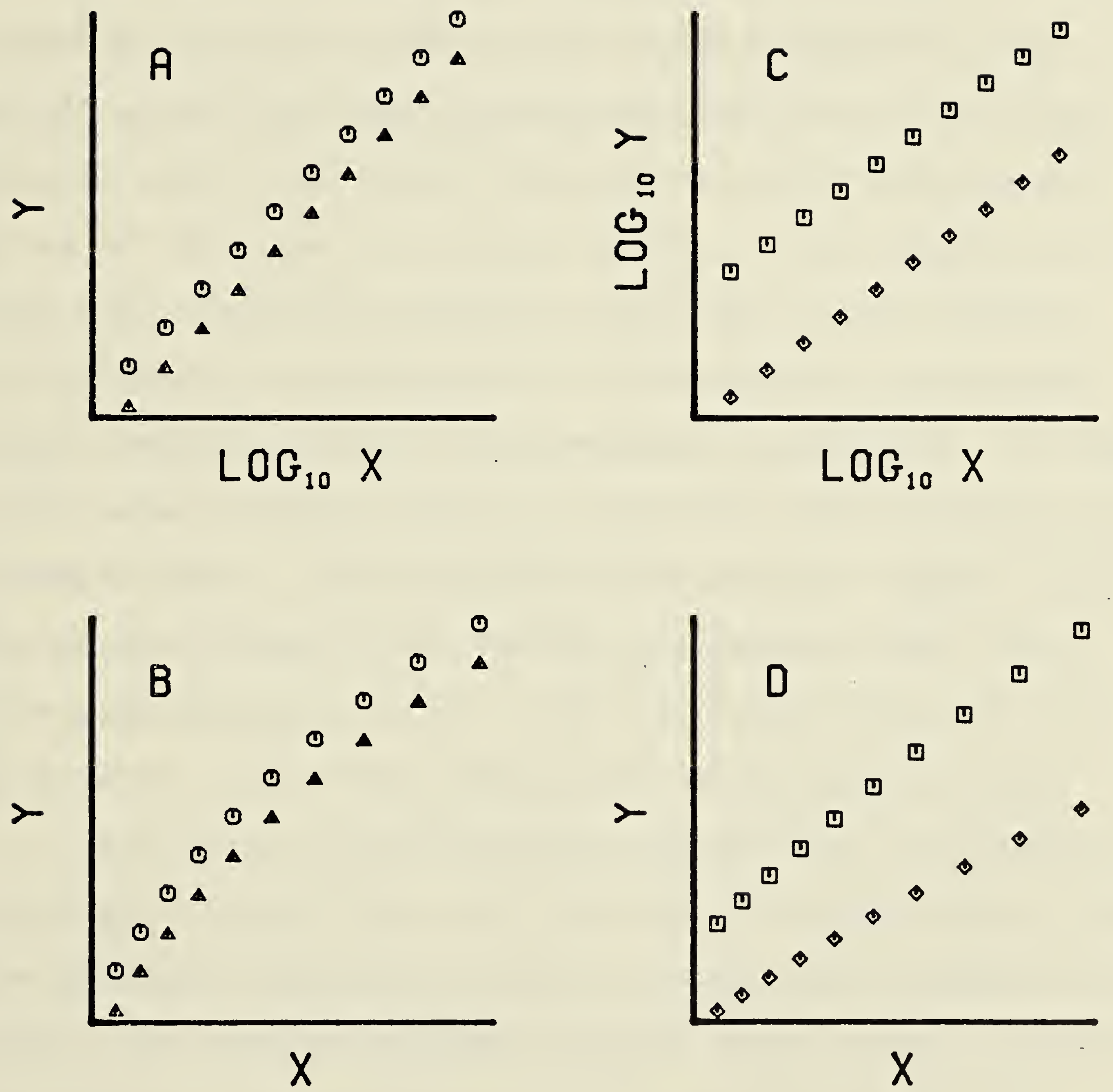
$F_s=5.238$ $0.01>p>0.005$ 2 and 102 df

Pure Mixed Windward
1.67 1.74 2.03 (based on t-tests p=0.05)

growth rate relationships revealed by analyses of covariance (Tables 10b, 11b, 12b and 13). In applying an analysis of covariance, several assumptions must be satisfied. If the variances under examination are not homogeneous, even following a suitable transformation, this test is inappropriate (Steel and Torrie 1960). Additionally, the linear regression equations explaining the association between the independent variable (age) and the dependent variable (DBH, height, or CI) for each of the samples must share a common slope. Failure to fulfill this requirement also invalidates the analysis of covariance, but in the present context the demonstrated interaction (i.e. different slopes) signifies different growth rates for the two groups of trees being compared.

The inability to demonstrate a difference between two means after adjusting for the affect of age suggests similar growth rates during all periods of development. If these means differed prior to adjustment for the effect of the independent variable (as demonstrated by a t-test), the inequality was probably due to a difference in age. A significant difference between the adjusted means may arise for two different reasons. If the dependent variable remains untransformed, disparity between means reveals dissimilar Y-intercepts for the regression equations (see Figure 5a and b). Since tree growth tends to follow a sigmoid curve (Husch <u>et</u> <u>al</u>. 1972) and the majority of trees were measured after they were greater than fifty years of age, extrapolation of the growth curves to age zero is

Figure 5. The effect of log transformation on growth curves. A and B are drawn from the regression equation used in the analysis of covariance comparing the height of Douglas fir trees in the leeward pure forests on the two study areas (Zoratti ▲ : Skelton ●). C and D are drawn from similar equations used in comparing the height of Douglas fir in the windward communities (Zoratti ◆ : Skelton ■).


A
Y
LOG10 X
C
LOG10 Y
LOG10 X
B
Y
X
D
Y
X

unrealistic. The observed difference therefore indicates unequal initial growth rates. Conversely, if both the dependent and independent variables were log transformed prior to analysis, the trees in question must have grown at perennially different rates (Figure 5c and d).

Douglas fir in both the windward and leeward communities on the Skelton area enjoyed superior rates of height growth (at least initially) relative to fir on the Zoratti area, even though there was no difference between areas in the rates of diameter growth. While Douglas fir grew more rapidly in diameter than pine in the windward communities, the interspecific difference in the leeward mixed community was not statistically significant. On both study areas, growth appears to have been most vigorous on leeward sites. The comparison of spruce and Douglas fir in the Zoratti leeward pure forest is unique in that spruce grew significantly faster in both DBH and height and also maintained a more rapid increase in conformation index.

Most of the transformations required by the analyses of covariance suggest that the trees on both study areas, with the possible exception of those in the Zoratti leeward mixed sites, are beyond the period of most rapid growth. Even on poor sites, interior Douglas fir reaches the point of inflection of the growth curve at about 40 years of age (Forestry Handbook for British Columbia 1971), after which the size of annual increments begins to decrease (Husch *et al.* 1972).

<u>Characteristics of Trees Used by Porcupines</u>

The relative proportions of used trees, as revealed by the presence of feeding scars, are an expression of the interspecific and interhabitat preferences of porcupines. Analysis of this information was based on a sample representing many years of feeding, so that the influence of individual preferences is suppressed and the resulting conclusions reflect only the majority response. These preferences are assumed to be constant through time.

Interspecific Preferences

Interspecific comparisons of the proportion of used trees suggest that porcupines that have inhabited the two study areas did not prefer one conifer species over another within a given community (Tables 14 and 15). This observation conflicts with the published accounts of porcupine food habits, which generally characterize this species as a selective feeder. The accuracy of many of these reports is, however, difficult to assess because data were not provided regarding the availability of the tree species involved and preference rankings are apparently subjective (Gabrielson 1928; Taylor 1935; Curtis and Kozicky 1944; Shapiro 1949). Two other studies describe interspecific preferences that are unsupported by the data presented. Gill and Cordes (1972) stated that limber pine was the preferred species in low elevation krummholz, similar to the windward communities described here, even

Table 14. Proportion of trees used within species and community categories from the Zoratti and Skelton study areas.

	Number Used	Number Not Used	% Used
Windward			
Zoratti			
P. menziesii	11	56	16.4
P. flexilis	96	274	25.9
Total	107	330	24.5
Skelton			
P. menziesii	37	217	14.6
P. flexilis	9	104	8.0
Total	46	321	12.5
Leeward Pure			
Zoratti			
P. menziesii			
High Density	119	76	61.0
Low density	124	59	67.8
Total	243	135	64.3
Picea spp.[1]	36	13	73.5
Skelton			
P. menziesii			
High Density	147	702	17.3
Low Density	164	205	44.4
Total	311	907	25.5
Leeward Mixed			
Zoratti			
P. menziesii	23	44	34.3
P. flexilis	22	72	23.4
Total	45	116	28.0

[1]Spruce and Douglas fir were not sampled with the same techniques (see Methods), consequently spruce does not participate in the Zoratti leeward pure total.

Table 15. Selected inter- and intraspecific comparisons of the proportion of trees used by porcupines on the two study areas. Each entry includes the log likelihood ratio statistic (G) and the probability of a similar or greater difference between groups. One degree of freedom is associated with each test.

	ZWF	ZPF	ZWP	ZMF	SWF
ZWP[1]	$G=2.448$, $p>0.1$				
ZPF	$G=53.203$, $p<0.005$				
ZPS		$G=1.276$, $p>0.1$			
ZMF	$G=4.836$, $0.05>p>0.025$	$G=19.649$, $p<0.005$			
ZMP			$G=0.140$, $p>0.5$	$G=1.793$, $p>0.1$	
SWF	$G=0.034$, $p>0.5$				
SWP			$G=17.970$, $p<0.005$		$G=2.706$, $p=0.1$
SPF		$G=182.568$, $p<0.005$			$G=14.584$, $p<0.005$

----

[1]Consult Table 9 for an explanation of the comparison codes.

though it was the only species available. Krefting *et al.* (1962) ranked the four major tree species on their Wisconsin study area according to porcupine use but re-analysis of these data indicate that the proportion of used trees does not vary statistically between species ($G=1.634$ $df=3$ $p>0.5$). Although porcupines in some areas do exhibit interspecific preferences (Curtis 1941 ; Rudolf 1949; Brander 1973) this habit is apparently not universal.

Individual trees are occasionally used during several years (see Tables 25 and 26). If these trees are weighted for the number of times they have been used, i.e. a tree used in two different years is recorded as two used trees, spruce were used proportionately more often than fir in the Zoratti leeward pure forest ($G=9.943$ $df=1$ $p<0.005$) and fir were used more frequently than pine in the Skelton windward community ($G=5.367$ $df=1$ $0.025>p>0.01$). However, it was not possible to weight trees for the number of times they were rejected by porcupines so that unused trees may be underrepresented.

Intercommunity Preferences

In contrast to this apparent lack of interspecific discrimination, porcupines on the Skelton and Zoratti areas exhibited marked community preferences (Tables 14, 15, and 16). Within a study area, the communities most amenable to tree growth received the greatest attention from porcupines. Douglas fir, in both the leeward pure and

[illegible]

[illegible]

[illegible]

[illegible]

Table 16. Selected intercommunity comparisons of the proportion of trees used by porcupines on the two study areas. Each entry includes the log likelihood ratio statistic (G) and the probability of a similar or greater difference between groups. One degree of freedom is associated with each test.

	Zoratti Windward	Zoratti Leeward Pure	Skelton Windward
Zoratti Leeward Pure	G=132.637 $p<0.005$		
Zoratti Leeward Mixed	G=0.567 $p>0.1$	G=59.639 $p<0.005$	
Skelton Windward	G=18.224 $p<0.005$		
Skelton Leeward		G=182.568 $p<0.005$	G=29.210 $p<0.005$

leeward mixed forests, were used proportionately more frequently than windward fir. The seeming preference for leeward pure fir over fir in the leeward mixed forests on the Zoratti area probably reflects the relative lengths of time these two communities have been subject to porcupine feeding rather than preferential utilization. As a whole, the Zoratti leeward mixed community was used in approximately equal proportion to the windward community because of an equivalent level of feeding on limber pine.

The relationship between use by porcupines and individual tree vigour has been widely documented (Rudolf 1949; Curtis and Wilson 1953; Krefting et al. 1962) and will be examined in more detail later. If the porcupines that have fed on the Zoratti and Skelton areas selected trees on the basis of vigour the collective response would be manifest in intercommunity preferences similar to those observed. Lack of interspecific preferences, in the light of differences in growth rates, suggests that the importance of vigour is not consistent between species. The influence of the intensive winds common in the windward communities on the selection of feeding trees by porcupines is uncertain, since Douglas fir in this community on the Zoratti area were used less frequently than leeward mixed fir, but limber pine in these two forest types were used in equivalent proportions.

Affirmation of intercommunity preferences is provided by the outcome of multiple regression analyses relating the

proportion of trees used by porcupines per plot to the proportion of Douglas fir per plot, plot density, slope, exposure, mean DBH, height, conformation index and age. Of these, the two variables that were the most effective predictors of the intensity of use on the two study areas (Table 17) also allowed the greatest discrimination between communities (Zoratti - proportion of Douglas fir/plot; Skelton - exposure). Variables that subsequently entered the equations were more useful in differentiating between stands within a vegetation type than between types.

Stand density is the most important single variable in explaining variation in the proportion of trees used within a plot, but because density is influential in determining the size, form and growth rate on both study areas, its role in food selection by porcupines may be multifaceted. Density may have been considered directly by porcupines feeding in at least the Zoratti windward community, as the dispersion of trees did not account for a significant proportion of variation in the size or form of either tree species (Tables 5, 6 and 7). The inverse relationship between density and the intensity of use, also reported by van Deusen and Myers (1962), may not be consistent throughout the range of possible densities, since Curtis and Wilson (1953) found that use increased with density in very dispersed stands of Ponderosa pine (Pinus ponderosa: mean density=3.32 trees/100 sq. m).

Table 17. Regression statistics describing the relationship between the proportion of trees used by porcupines per plot and various plot attributes. Additional statistics have been provided in Appendix 3.

	Independent Variables	Beta	R^2	p
Windward				
Zoratti (9)[2]	Density {4}[1]	0.744	0.553	0.025>p>0.01
Skelton (11)				p>0.05
Leeward Pure				
Zoratti {5} (12)	Density {1}[3]	-0.833	0.499	0.05>p>0.025
	Slope {4}	-0.690		
Skelton (29)	Density {3}	-0.500	0.717	p<0.001
	Slope {3}	0.396		
	Exposure {1}	0.307		
Leeward Mixed				
Zoratti (5)	#fir/#total	0.958	0.917	0.025>p>0.01
Combined				
Zoratti (27)	#fir/#total	0.456	0.713	p<0.001
	Mean DBH {2}	0.429		
Skelton (40)	Exposure {1}[4]	0.479	0.628	p<0.001
	Density {4}	0.492		
	Slope {4}	-0.235		

[1]Numbers in braces refer to the type of transformation applied: {1} squared; {2} square root; {3} log; {4} inverse, {5} arcsin. Braces following the study area name indicate that the transformation was applied to the dependent variable.
[2]Sample size.
[3]Proportion of Douglas fir was the first independent variable to enter this equation, but it dropped out after the addition of slope.
[4]Mean DBH was the first independent variable to enter this equation, but it dropped out after the addition of density.

The role of slope in the selection of stands in the leeward pure forests is unclear because slope is apparently not important in explaining variation in tree stature (Tables 5, 6 and 7). Slope could be related to an aspect of porcupine biology other than feeding, or it could be highly correlated with unmeasured factors that influence porcupines more directly. Although van Deusen and Myers (1962) reported a similar correlation between slope and the proportion of used trees, they likewise offered no explanation of its importance.

The regression analysis for the Zoratti leeward mixed forest is presented with reservation. Although the proportion of Douglas fir per plot was the only variable to explain a significant portion of the variation in the intensity of use, a thorough analysis was not possible because the number of variables in the equation rapidly approached the number of observations (Draper and Smith 1966). The proportion of fir per plot was also the first variable to enter the regression equation in the Zoratti leeward pure analysis, but it was removed from the equation following the addition of density and slope because it had ceased to make a significant contribution to the explanation of variation.

Study Area Differences

The Zoratti area has been more extensively used by porcupines (Tables 14 and 16) than the Skelton area, but

because individual porcupines probably could not have exercised a choice between these two areas, inferences regarding the relative quality of these forests would probably be unfounded. Taylor (1935) stated that the prevalence of porcupine feeding in a particular forest is primarily determined by the number of porcupines present, which is greatly affected by the physical location of the forest and need not be related tc the type of trees available. Both Taylor (1935) and van Deusen and Myers (1962) have reported that trees on the periphery of a forest receive the greatest attention from porcupines and that this habit was related to the proximity of the forest edge to summer feeding areas. The Zoratti area is a narrow, linear ridge parallelling the edge of the prairie so that the entire forest is essentially peripheral, whereas the Skelton area lies perpendicular to the prairie and is a larger, more continuous block of timber. This difference in size and orientation may explain the difference in utilization between the two areas.

Individual Tree Preferences - Relative

The preferential use of a specific community or type of stand by porcupines ultimately depends upon the deliberate use of individual trees. Comparison of the size and conformation of used trees relative to unused trees could disclose the existence and form of porcupine preferences. The average position of each tree in relation to the

community mean, during the 20 years prior to measurement, has been examined rather than the tree's absolute size or age because, with the exception of the leeward pure forests, only a small proportion of the available trees was used by porcupines during a given year. Z-transformations ($X_i - \bar{X}/s$; Sokal and Rohlf 1969) of age, DBH, height and conformation index were calculated for each tree for each of the 20 years prior to measurement. The average transformation of the four variables for each tree during this period is a measure of its relative status in the community, measured in standard deviations from the mean of zero.

Porcupines have used trees that were commonly larger and had more extensive crowns than the trees they neglected (Tables 18a, 19a and 20a), even though these trees were generally not older than unused trees (Table 21). Although analyses of covariance could not be applied universally, the results indicate that the trees used by porcupines were faster growing than unused trees (Tables 18b, 19b and 20b), an observation which has been widely reported (Rudolf 1949; Curtis and Wilson 1953; Krefting _et al_. 1962; Spencer 1964). Discriminant analyses (Table 22) indicate that DBH and growth form are more effective than age or height at distinquishing used trees from unused trees and suggest that any tendency for used trees to be older or taller was an artifact of the strong intercorrelations between all four variables.

Table 18. Comparisons of the relative diameters at breast height of porcupine feeding trees with unused trees on the Zoratti and Skelton areas. The sizes of used and unused limber pine in the Skelton windward community were not compared because only two trees were used during the 20 years preceding measurement.

		a) t-test				Adjusted	b) Analysis of Covariance				
		Means	t	p	df and Type	Means	F[1]	p	F[2]	p	df
ZWF[3]	used	0.57				[4]					
			2.58	0.02>p>0.01	65 P						
	unused	-0.28									
ZPF	used	0.19				[4]					
			5.51	p<0.001	379 P						
	unused	-0.37									
ZMF	used	1.08				0.48					1
			4.99	p<0.001	66 P		4.326	0.05>p>0.025	80.282	p<0.001	
	unused	-0.42				-0.10					25
ZPS	used	0.30				[5]					
			4.14	p<0.001	47 P						
	unused	-0.84									
ZWP	used	0.32				0.28					1
			1.79	p>0.05	51 S		4.277	0.05>p>0.025	47.710	p<0.001	
	unused	-0.08				-0.06					106
ZMP	used	0.88				[5]					
			3.69	p<0.001	94 P						
	unused	-0.27									
SWF	used	0.91				1.56					1
			4.13	p<0.001	252 P		15.841	p<0.001	11.269	0.005>p>0.001	
	unused	-0.07				-0.16					50
SPF	used	0.83				0.63					1
			12.46	p<0.001	1219 P		27.518	p<0.001	165.301	p<0.001	
	unused	-0.18				-0.08					240

[1]This F-test examines the equality of the adjusted means.

[2]This F-test examines the contribution of age in explaining variation in DBH.

[3]Explanation of this comparison code is provided in Table 9.

[4]The t-test comparing the DBH of aged used and unused trees provides different results from part a) of this table. The aged trees are therefore considered an unrepresentative sample of DBH.

[5]This analysis was not performed because of a small sample (< 5) of aged, used trees.

Table 19. Comparisons of the relative heights of porcupine feeding trees with unused trees on the Zoratti and Skelton areas. The sizes of used and unused limber pine in the Skelton windward community were not compared because only two trees were used during the 20 years preceding measurement.

		a) t-test				Adjusted	b) Analysis of Covariance				
		Means	t	p	df and Type	Means	F[1]	p	F[2]	p	df
ZWF[3]	used	0.30				-0.15					1
			1.51	p>0.1	64 P		0.252	p>0.5	11.372	0.005>p>0.001	
	unused	-0.21				0.06					22
ZPF	used	0.14									
			3.93	p<0.001	309 S	Heterogeneous variances					
	unused	-0.30									
ZMF	used	1.00				0.43					1
			4.41	p<0.001	65 P		1.931	p>0.1	24.786	p<0.001	
	unused	-0.38				-0.10					24
ZPS	used	0.27				[4]					
			3.54	0.01>p>0.001	44 P						
	unused	-0.77									
ZWP	used	0.31				[5]					
			2.05	0.05>p>0.02	53 S						
	unused	-0.08									
ZMP	used	0.62				[4]					
			2.56	0.02>p>0.01	77 P						
	unused	-0.25									
SWF	used	0.77									1
			3.49	p<0.001	236 P	Significant interaction[6]			5.254	0.05>p>0.025	
	unused	-0.07									44
SPF	used	0.34									
			5.03	p<0.001	1126 P	Heterogeneous variances					
	unused	-0.11									

[1]This F-test examines the equality of the adjusted means.
[2]This F-test examines the contribution of age in explaining variation in height.
[3]Explanation of this comparison code is provided in Table 9.
[4]This analysis was not performed because of a small sample (< 5) of aged, used trees.
[5]The t-test comparing the height of aged used and unused trees provides different results from part a) of this table. The aged trees are therefore considered an unrepresentative sample of height.
[6]The following F-value represents the significance test for interaction.

Table 20. Comparisons of the relative conformation indices of porcupine feeding trees with unused trees on the Zoratti and Skelton areas. The form of used and unused limber pine in the Skelton windward community was not compared because only two trees were used during the 20 years preceding measurement.

		a) t-test			df and Type	Adjusted Means	b) Analysis of Covariance				
		Means	t	p			F[1]	p	F[2]	p	df
ZWF[3]	used	0.58									
			1.87	p>0.05	10 S	Heterogeneous variances					
	unused	-0.34									
ZPF	used	0.25				0.24					1
			6.58	p<0.001	339 P		9.257	0.005>p>0.001	21.420	p<0.001	
	unused	-0.45				-0.26					101
ZMF	used	0.70				[4]					
			3.28	0.01>p>0.001	65 P						
	unused	-0.44									
ZPS	used	0.28				[5]					
			3.65	p<0.001	44 P						
	unused	-0.77									
ZWP	used	0.18				0.32					1
			1.33	p>0.1	54 S		4.067	0.05>p>0.025	56.091	p<0.001	
	unused	-0.08				-0.07					93
ZMP	used	0.93				[5]					
			3.82	p<0.001	77 P						
	unused	-0.33									
SWF	used	0.35				[4]					
			1.56	p>0.1	236 P						
	unused	-0.03									
SPF	used	0.97									1
			12.34	p<0.001	182 S	Significant interaction[6]			15.087	p<0.001	
	unused	-0.21									220

[1] This F-test examines the equality of the adjusted means.
[2] This F-test examines the contribution of age in explaining variation in conformation index.
[3] Explanation of this comparison code is provided in Table 9.
[4] The t-test comparing the conformation index of aged used and unused trees provides different results from part a) of this table. The aged trees are therefore considered an unrepresentative sample of conformation index.
[5] This analysis was not performed because of a small sample (< 5) of aged, used trees.
[6] The following F-value represents the significance test for interaction.

Table 21. Comparisons of the relative ages of porcupine feeding trees with unused trees on the Zoratti and Skelton areas. The ages of used and unused limber pine in the Skelton windward community were not compared because only two trees were used during the 20 years preceding measurement.

	Means	t	p	df	Type
ZWF[1] used	0.26	0.81	p>0.4	23	P
unused	-0.10				
ZPF used	0.05	0.58	p>0.5	87	S
unused	-0.06				
ZMF used	0.73	2.02	p>0.05	26	P
unused	-0.24				
ZWP used	-0.26	1.61	p>0.1	38	S
unused	0.05				
ZMP used	1.05	2.46	0.05>p>0.02	28	P
unused	-0.19				
ZPS used	-0.17	0.80	p>0.4	6	P
unused	0.50				
SWF used	0.19	0.44	p>0.5	51	P
unused	-0.02				
SPF used	0.40	2.98	0.01>p>0.001	43	S
unused	-0.06				

[1]Explanation of this comparison code is provided in Table 9.

Table 22. Discriminant analysis statistics detailing the measured variables that best distinguished between porcupine feeding trees and unused trees on the Zoratti and Skelton areas.[1]

	Independent Variable[2]	Constant	Discriminant Coefficient	Wilks' Lambda	Chi-square (1 df)	p
ZWF[3]	CI (56,10)	0.194	0.952	0.900	6.682	0.01>p>0.005
ZPF	CI (159,182)	0.077	0.968	0.887	40.698	p<0.001
ZMF	DBH (58,9)	0.212	1.023	0.728	20.499	p<0.001
ZPS	DBH (13,33)	0.012	0.970	0.697	15.678	p<0.001
ZWP	DBH (266,45)	0.026	0.959	0.976	7.593	0.01>p>0.005
ZMP	CI (69,10)	0.164	0.944	0.841	13.259	p<0.001
SWF	DBH (220,18)	-0.004	1.018	0.931	16.968	p<0.001
SPF	CI (997,151)	0.051	0.971	0.847	183.083	p<0.001

[1]Discriminant analyses were first performed on aged trees only, but because age was not an effective discriminator the analyses presented are based on all trees.
[2]Bracketed quantities represent the number of unused and used trees during the 20 year period preceding measurement.
[3]Explanation of this comparison code is provided in Table 9.

In addition to increased shoot and xylem growth, vigorous trees produce a larger annual increment of phloem than suppressed trees (Bannan 1955; Grillos and Smith 1959). Rapidly growing trees with large open crowns therefore provide more potential food for porcupines because they support more foliage and a greater volume of inner bark than crowded trees. Porcupines generally feed on inner bark that is accessible from positions that can be maintained without undue exertion (Taylor 1935; Spencer 1964). This type of tree, which is characterized by more large branches, would therefore allow porcupines greater access to the potential food.

Diameter at breast height and conformation index both incorporate information about crown width and stem diameter and relate a measure of the potential food in a tree and its accessibility. A porcupine that was cognizant of this relationship could therefore assess at least the quantity of food available in a given tree without having to expend energy climbing it. Presumably, trees can become too large to be successfully climbed (Taylor 1935; Curtis and Kozicky 1944; Curtis and Wilson 1953), resulting in a decline in their use by porcupines even though they contain large quantities cf high quality food.

Individual Tree Preferences - Absolute

Only trees in the leeward pure forests were fed upon with sufficient frequency to allow an examination of the

absolute size of used trees. The tendency for porcupines to use trees that were larger than unused trees (Figures 6-11) has already been noted. Although the mean DBH, height and growth form of used trees in the Zoratti forest increased through the 20 years prior to measurement, the average DBH and height in the Skelton forest remained relatively constant (Table 23 and Figures 6-11).

The average diameters of used trees from both study areas fall within the range of size preferences reported from various regions of North America (Taylor 1935; Curtis and Wilson 1953; Krefting *et al*. 1962; van Deusen and Myers 1962). The predilection of porcupines for a specific size class of tree irrespective of geographic location or the species of tree involved, lends support to the suggestion of Curtis and Wilson (1953) that porcupines may be most adept at climbing trees between 15 and 25 cm DBH; a physical limitation which could have several consequences on the pattern of forest use. If porcupines favoured a particular size of tree, the scope for additional discrimination on the basis of other attributes, such as vigour, would be reduced. In a relatively even-aged forest, vigorous trees of the appropriate dimensions would only be available for a short period of time relative to the existence of the forest and the intensity of porcupine use would be expected to peak and then decline as vigorous trees became too large to climb.

Figure 6. Means and standard errors of the diameters at breast height of Douglas fir used (right bar of each pair) and not used by porcupines in the leeward pure forest on the Zoratti study area for each of the 20 years prior to measurement. Also included for each year are the number of used and unused trees. An asterisk denotes a statistically significant difference ($p \leq 0.05$) between means as determined by a t-test. All t-tests employed a pooled variance estimate.

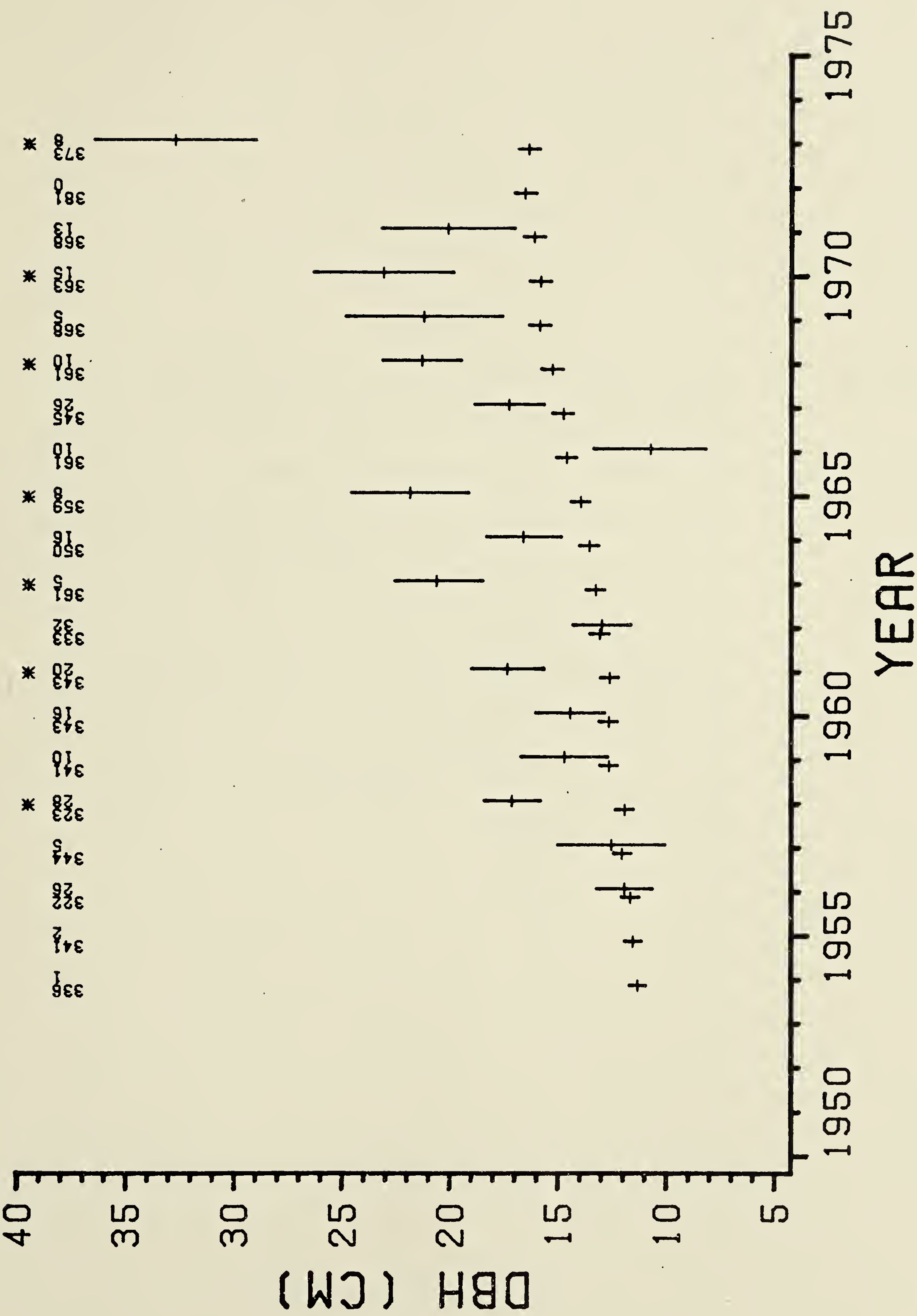
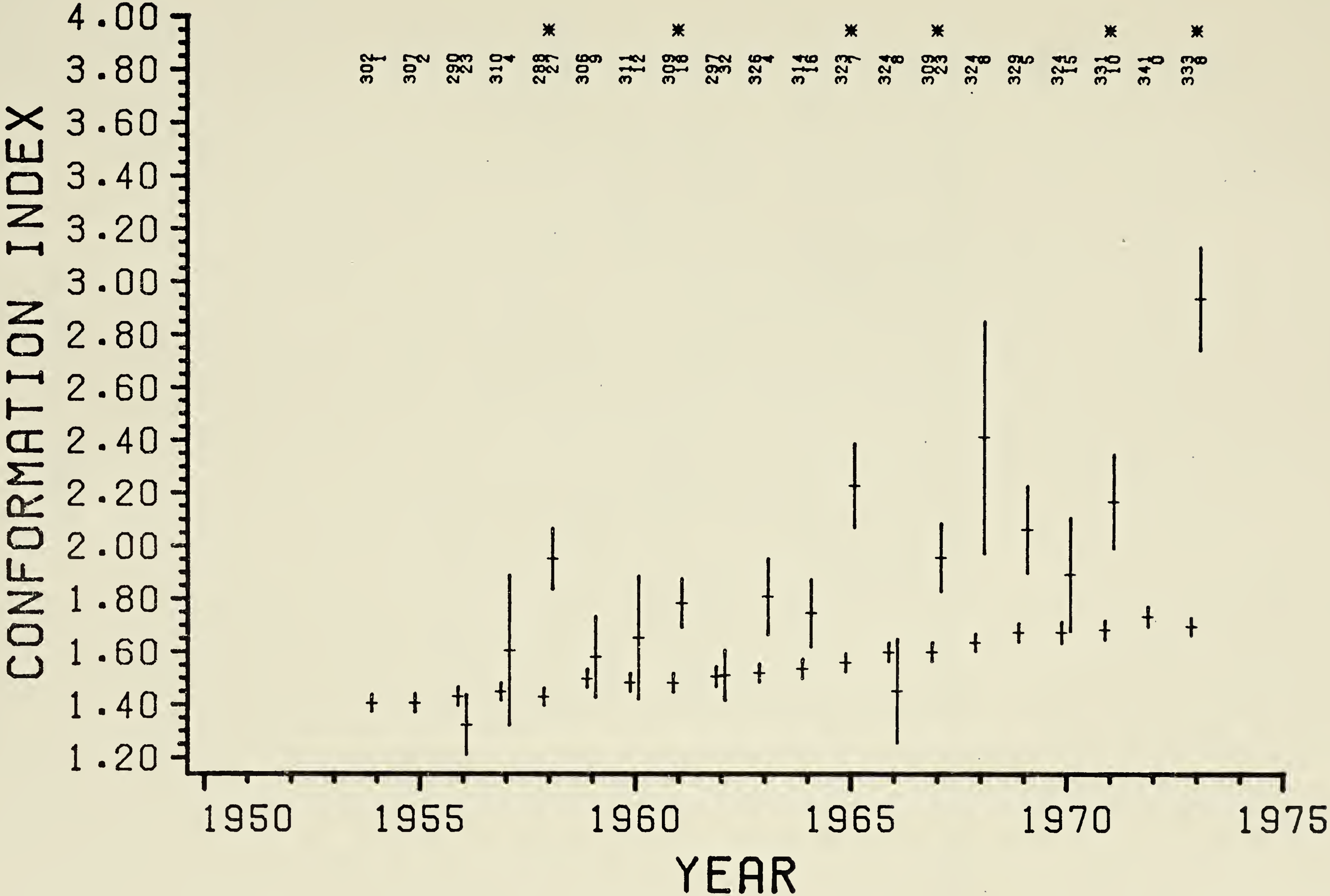

DBH (CM)
40
35
30
25
20
15
10
5
YEAR
1950
1955
1960
1965
1970
1975
339 1
341 2
322 26
344 5
323 28
341 10
343 16
343 20
333 32
361 5
350 16
359 8
361 10
345 26
361 10
368 5
363 15
368 13
381 0
373 8

Figure 7. Means and standard errors of the heights of Douglas fir used (right bar of each pair) and not used by porcupines in the leeward pure forest on the Zoratti study area for each of the 20 years prior to measurement. Also included for each year are the number of used and unused trees. An asterisk denotes a statistically significant difference ($p \leq 0.05$) between means as determined by a t-test. All t-tests employed a pooled variance estimate.


HEIGHT (M)
YEAR
1950
1955
1960
1965
1970
1975
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19

Figure 8. Means and standard errors of the conformation indices of Douglas fir used (right bar of each pair) and not used by porcupines in the leeward pure forest on the Zoratti study area for each of the 20 years prior to measurement. Also included for each year are the number of used and unused trees. An asterisk denotes a statistically significant difference ($p \leq 0.05$) between means as determined by a t-test. All t-tests employed a pooled variance estimate.


CONFORMATION INDEX
4.00
3.80
3.60
3.40
3.20
3.00
2.80
2.60
2.40
2.20
2.00
1.80
1.60
1.40
1.20
YEAR
1950
1955
1960
1965
1970
1975
302 1
307 2
290 23
310 4
288 27
306 9
311 12
309 18
297 32
326 4
314 16
323 7
324 8
309 23
324 8
329 5
324 15
331 10
341 0
333 8

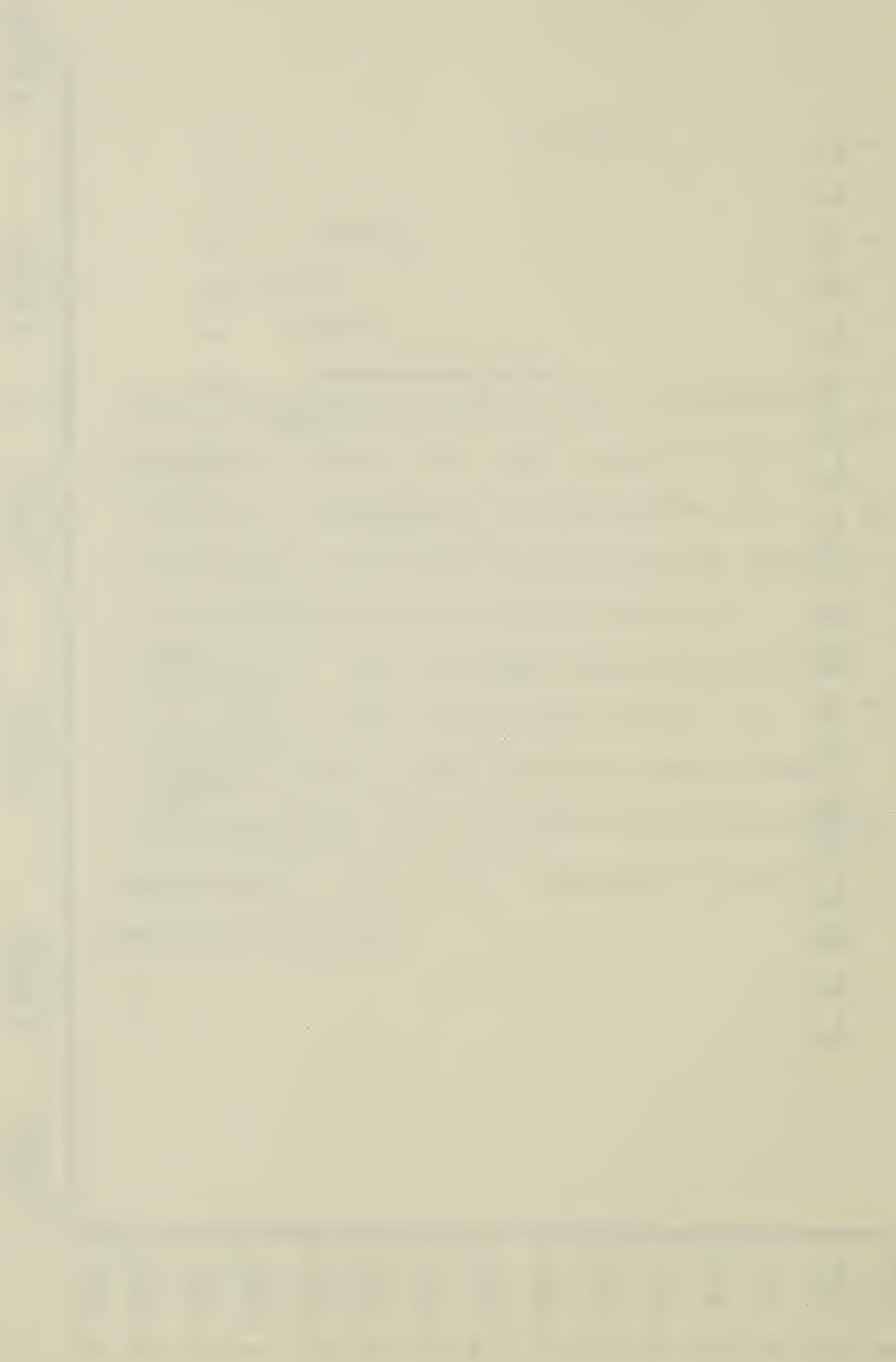
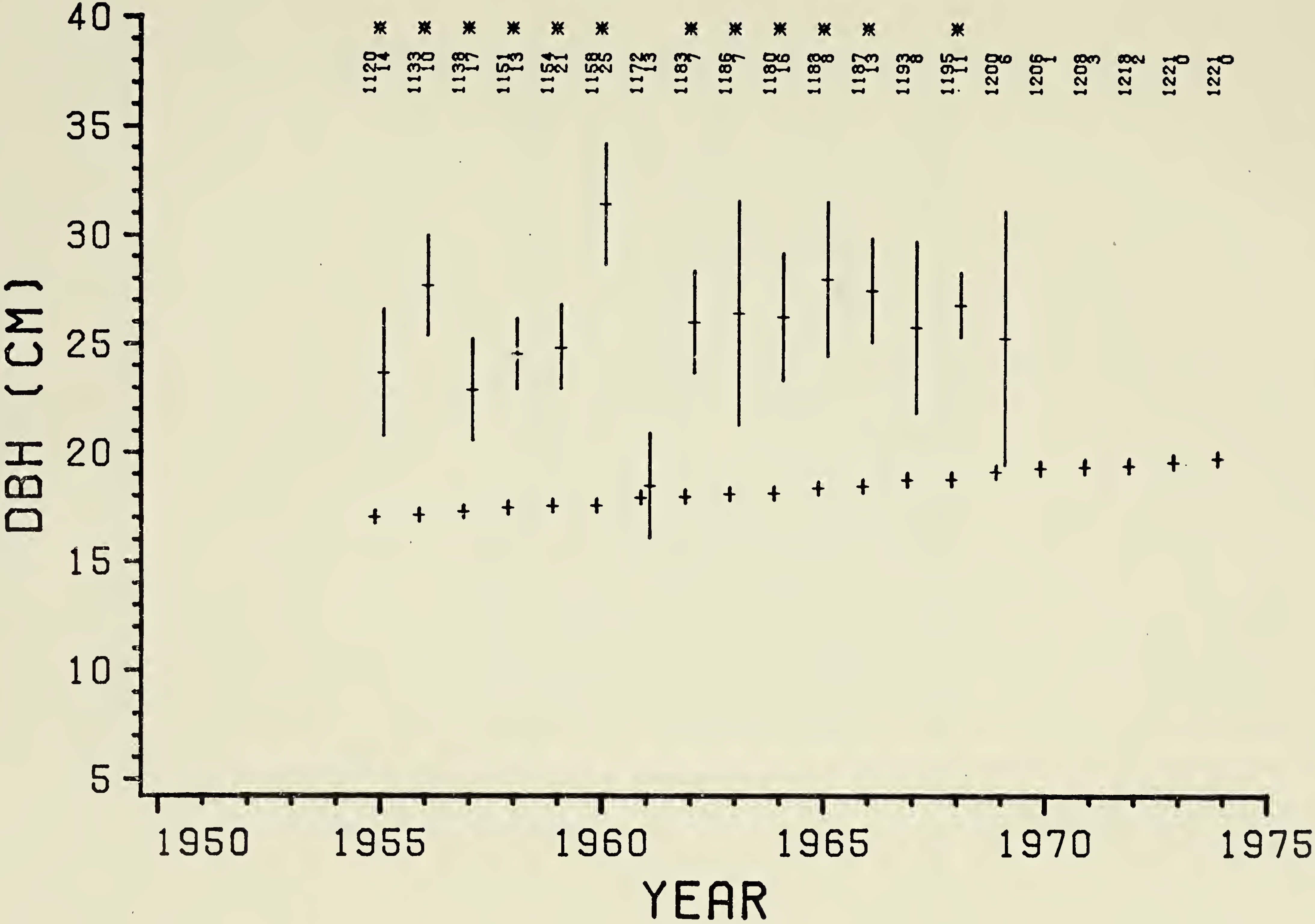


Figure 9. Means and standard errors of the diameters at breast height of Douglas fir used (right bar of each pair) and not used by porcupines in the leeward pure forest on the Skelton study area for each of the 20 years prior to measurement. Also included for each year are the number of used and unused trees. An asterisk denotes a statistically significant difference ($p \leq 0.05$) between means as determined by a t-test. All t-tests employed a pooled variance estimate.



DBH (CM)
40
35
30
25
20
15
10
5
1950
1955
1960
1965
1970
1975
YEAR

Figure 10. Means and standard errors of the heights of Douglas fir used (right bar of each pair) and not used by porcupines in the leeward pure forest on the Skelton study area for each of the 20 years prior to measurement. Also included for each year are the number of used and unused trees. An asterisk denotes a statistically significant difference ($p \leq 0.05$) between means as determined by a t-test. All t-tests employed a pooled variance estimate.

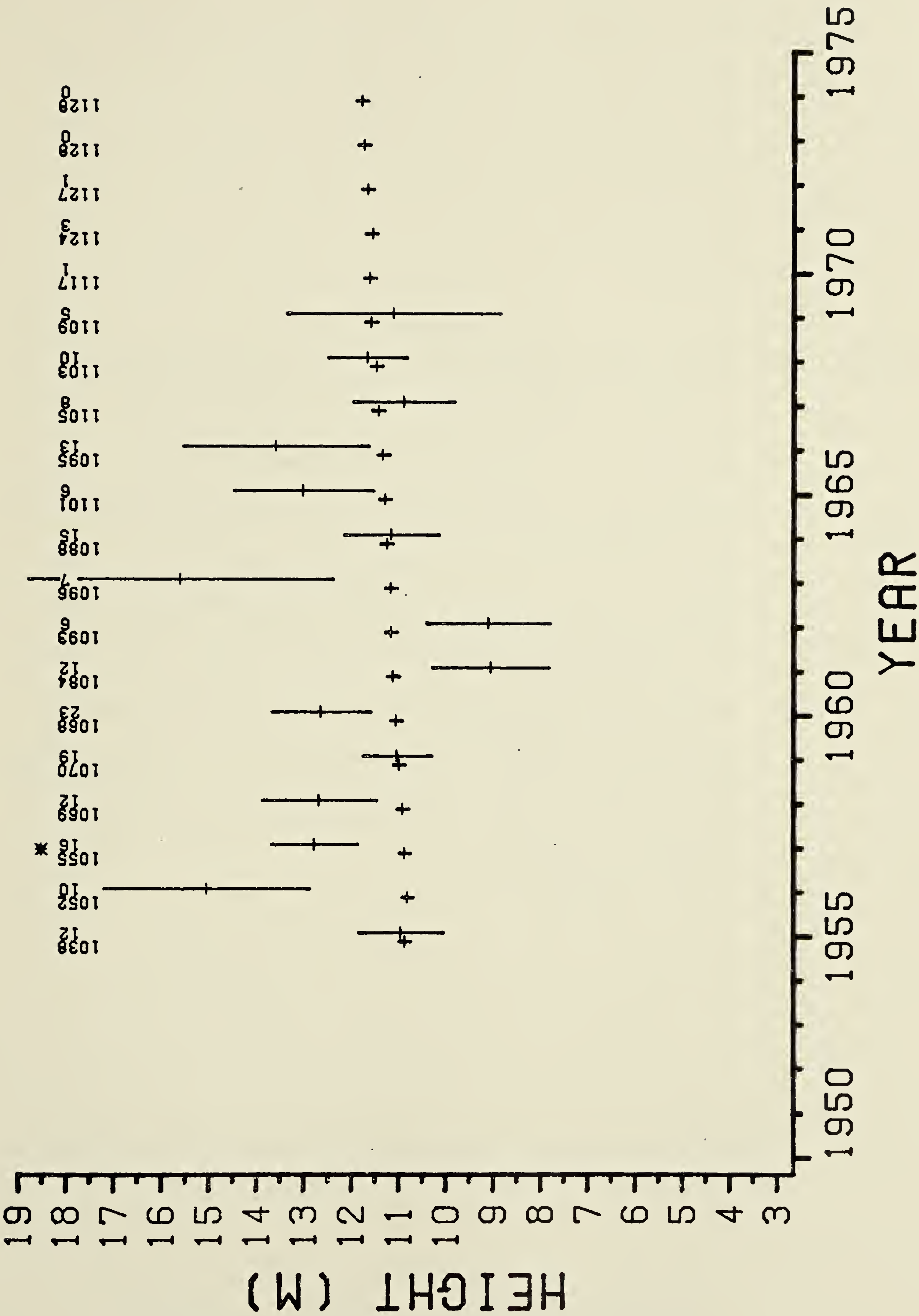

YEAR
1950
1955
1960
1965
1970
1975
HEIGHT (M)
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19

Figure 11. Means and standard errors of the conformation indices of Douglas fir used (right bar of each pair) and not used by porcupines in the leeward pure forest on the Skelton study area for each of the 20 years prior to measurement. Also included for each year are the number of used and unused trees. An asterisk denotes a statistically significant difference ($p \leq 0.05$) between means as determined by a t-test. All t-tests employed a pooled variance estimate.

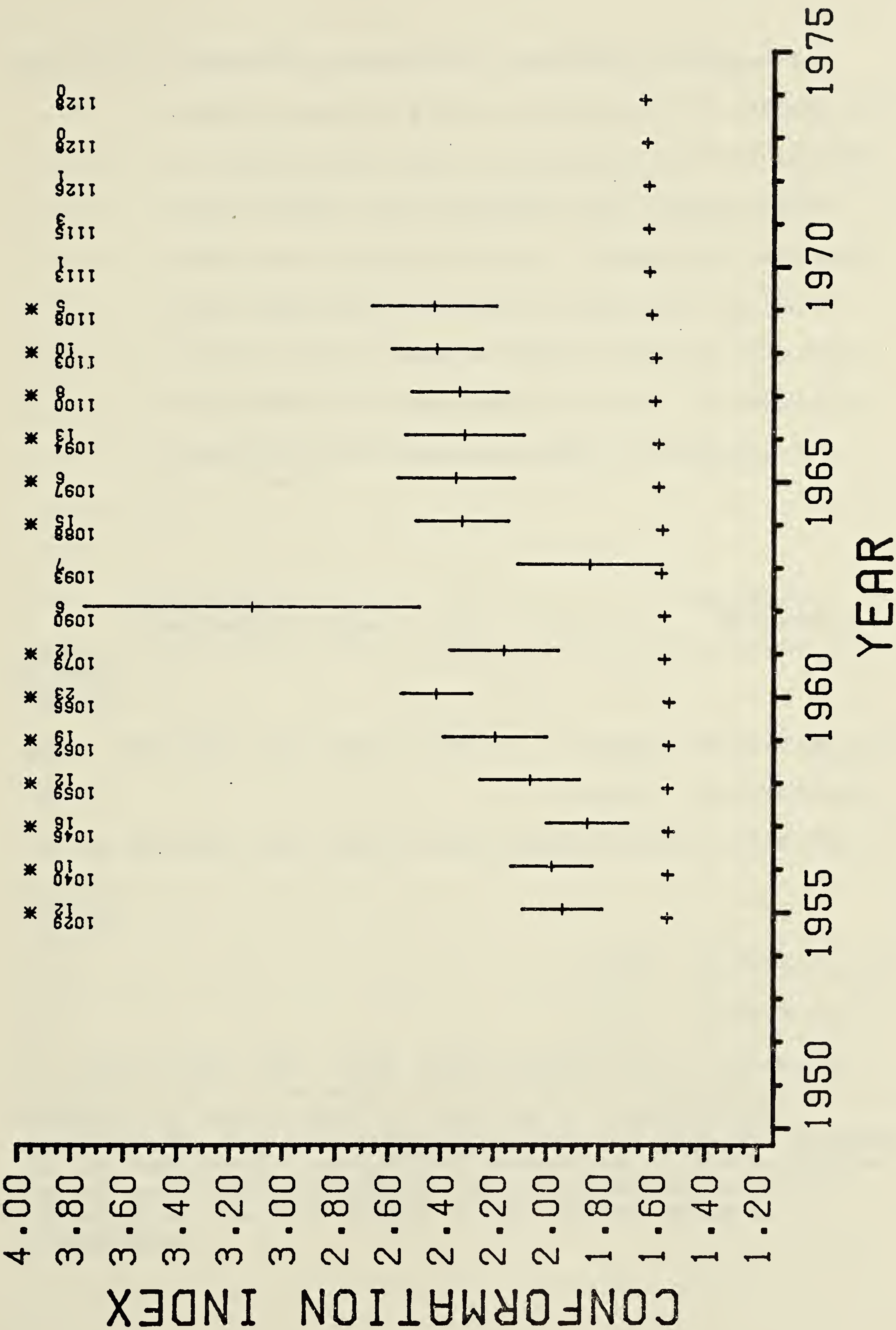

CONFORMATION INDEX
4.00
3.80
3.60
3.40
3.20
3.00
2.80
2.60
2.40
2.20
2.00
1.80
1.60
1.40
1.20
YEAR
1950
1955
1960
1965
1970
1975

Table 23. Regression statistics describing attempts to explain year to year variation in the average size of Douglas fir used by porcupines in the leeward pure forests on the Zoratti and Skelton study areas (see Figures 6-11). Independent variables that could have entered the equation included use age, the number of plots used per year and the number of trees used per year. Additional statistics have been provided in Appendix 3.

	Independent Variable[1]	Beta	R^2	p	Weighted Mean±se[2]
Zoratti (n=17)					
DBH	Use Age {3}	-0.831	0.690	p<0.001	16.11±0.645 cm
Ht				p>0.05	9.12±0.298 m
CI {1}	Use Age {4}	-0.487	0.238	0.05>p>0.025	1.75±0.056
Skelton (n=16)					
DBH				p>0.05	25.96±0.799 cm
Ht				p>0.10	12.00±0.408 m
CI {4}	Use Age {4}	0.526	0.277	0.05>p>0.025	2.24±0.056

[1]Numbers in braces refer to the type of transformation applied: {1} squared; {2} square root; {3} log; {4} inverse.
[2]If age explained a significant proportion of the variation in the particular attribute, the corresponding mean was adjusted so that the effect of age between years is negligible.

[illegible]

[illegible]

[illegible]

[illegible]

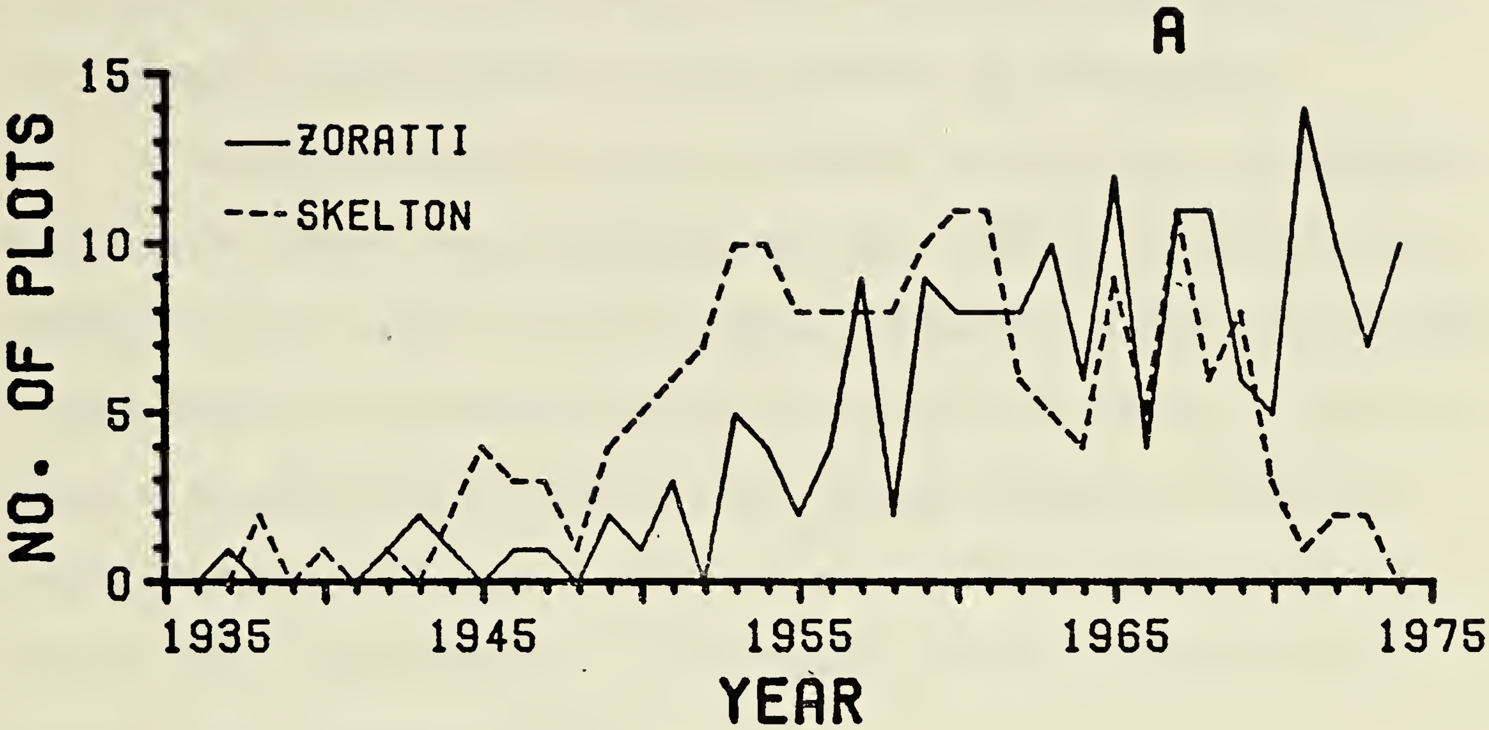
Trees used by porcupines in the Skelton leeward forest, during the 20 years prior to measurement, were generally larger than the trees used on the Zoratti area during the same period (DBH $t=9.647$ $p<0.001$ P df=31: height $t=5.750$ $p<0.001$ P df=31: CI $t=6.156$ $p<0.001$ P df=31: Table 23). If porcupines exercised size preferences solely related to the ease of climbing trees, local differences in the size of used trees of the magnitude observed would not be expected unless the preferred size was unavailable. Although trees on the Skelton area were generally larger than on the Zoratti area (Table 8), this difference is not sufficient to explain the disparity in the size of used trees. The relatively greater intensity of porcupine feeding on the Zoratti area (Table 14) may have forced some animals to use trees smaller than the preferred size. Storm and Halvorson (1967) presented convincing evidence that the removal of bark by porcupines greatly affects the vigour of a tree for up to ten years so that in a forest that has been heavily used for several years, the number of rapidly growing trees within the preferred size class would be reduced and porcupines would be faced with a choice between slower growing trees of the appropriate size or smaller vigorous trees. Election between these two alternatives would depend upon the relative significance of tree size and vigour to porcupines and upon a porcupine's ability to recognize indicators of vigour such as the amount of annual branch extension or the quantity of recent needles.

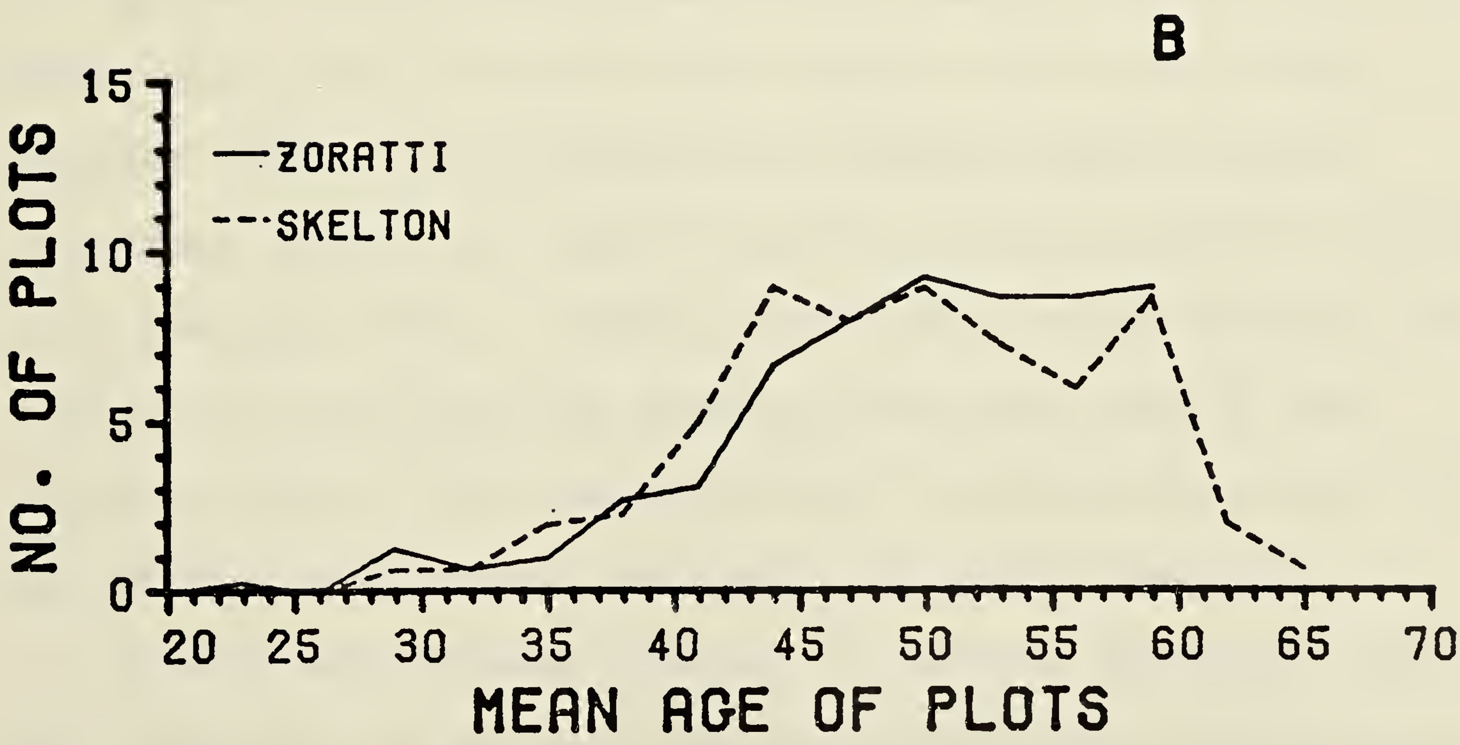
<u>Temporal Changes in the Intensity of Use</u>

The number of plots used per year can be regarded as an index of the number of porcupines present on a study area per winter. Considering this index of porcupine numbers for a period of several decades should provide an indication of the number of porcupines inhabiting the study areas through time. This index is probably more reliable than an index based on the number of individual trees used per year since individual porcupines tend to concentrate their feeding, during a single winter, in a very small area (Spencer 1964) and the number of used trees counted for a particular winter would be greatly affected by the location of the sampling plots with respect to these "feeding pockets".

Figure 12a illustrates that the intensity of use of an area by porcupines is not consistent through time. If the short-term fluctuations are smoothed by plotting three year means and the curves are shifted so that the mean ages of the forests are equivalent, the two curves follow one another quite closely (Figure 12b: $r=0.922$ $r^2=0.850$ $p<0.001$ $n=14$). The final drop of the Skelton curve (Figure 12b) would seem to predict a similar decline in porcupine numbers on the Zoratti study area. During the winter (1974-1975) following the collection of the plot data from which the Zoratti curve was drawn only three porcupines were found. No porcupines could be located on this area during the subsequent winter (1975-1976). This decrease in porcupine numbers may, however, have been premature because the

Figure 12. The relationship between time and the intensity of feeding by porcupines on the Zoratti and Skelton study areas. The upper graph (a) depicts the number of plots used on each area per year and the lower graph (b) illustrates the numbers of plots used in relation to the mean age of the forest.


A
15
10
5
0
NO. OF PLOTS
—ZORATTI
---SKELTON
1935
1945
1955
1965
1975
YEAR


B
15
10
5
0
NO. OF PLOTS
—ZORATTI
---SKELTON
20
25
30
35
40
45
50
55
60
65
70
MEAN AGE OF PLOTS

landowner of this study area had been shooting porcupines for several years prior to the winter of 1974-1975.

A similar trend is also evident in the data presented by Crouch (1969) and Krefting et al. (1962), although the timing of the peak in use varies. Spencer (1964) described three peaks in porcupine use, separated by 20 to 30 years, from a large area of piñon pine (Pinus edulis) forest in south-western Colorado, but did not reveal whether these peaks were experienced in all parts of the forest or in stands of a similar size or age.

Changes in the average number of porcupines feeding on both study areas could have been completely independent of the quality of the habitat. Nothing is known of the activities of these porcupines during any season but the winter, although numerous studies have reported that porcupines frequent different areas during summer and winter (Gabrielson 1928; Taylor 1935; Curtis and Wilson 1953; Brander 1973). The condition of summer habitats could therefore affect the number of porcupines in winter habitats (see Fretwell 1972), but the close association between the number of plots used per year and the mean ages of the forests (Figure 12b) suggests that the intensity of use of the winter habitats was dependent on their quality.

These observations support an earlier suggestion that the intensity of use in a forest should rise and fall as the size of vigorous trees passed through the range of sizes preferred by porcupines. The observed decline in the

intensity of porcupine use of both study areas could have further resulted from the concurrent reduction of vigour associated with ageing in the entire forest. An additional implication of these findings is that local changes in the basic population size of porcupines may be the result of selection of a "better" habitat rather than changes in natality or mortality.

Characteristics of Porcupine Feeding

Repeated Feeding in Individual Trees

Use of a particular tree during a given winter may influence its further use by porcupines in subsequent years. Several studies have reported that porcupines return to the same tree year after year, often enlarging old scars (Curtis 1941; Shapiro 1949; Spencer 1964). Although porcupines may select trees that have been used in the past, repeated use of individual trees could have been a random event. The latter suggestion can be tested by examining the goodness of fit between a Poisson distribution and the group frequencies of trees classed according to the number of years that they were fed upon by porcupines (see Sokal and Rohlf 1969).

With the exceptions of Douglas fir in the leeward pure forests, the trees on both study areas were used from year to year in a random fashion (Tables 24 and 25). This implies that even though there was a preferred type of tree, as shown earlier (Tables 18, 19 and 20), there were enough of that type that they could be used in a manner independent of previous use. Curtis and Wilson (1953) also examined this relationship statistically and came to a similar conclusion.

Douglas fir in the leeward pure forests were used in contrasting patterns on the two study areas. Individual trees in low density stands on both areas were used during

Table 24. The frequency of repeated use of individual trees on the Zoratti study area. The log likelihood ratio tests (G) are based on a comparison between the observed frequencies (f) and the expected frequencies ($\hat{f}$) of a similar population (i.e. identical mean) with a Poisson distribution. The degrees of freedom associated with this goodness of fit test are the number of classes - 2 (Sokal and Rohlf 1969), so that this test is inappropriate for less than three classes.

# Years Used	Windward Fir f	Windward Fir $\hat{f}$	Windward Pine f	Windward Pine $\hat{f}$	Windward Total f	Windward Total $\hat{f}$	Leeward Pure Fir f	Leeward Pure Fir $\hat{f}$
0	56	56.0	303	305.4	359	361.7	202	222.7
1	10	10.0	63	58.6	73	68.4	194	155.7
2	1	0.9	4	5.6	5	6.5	39	54.4
3							11	12.7
4							2	2.2
n	67		370		437		448	
$\bar{X}$	0.179		0.192		0.189		0.699	
G	[1]		1.627		1.535		16.602[2]	
df			1		1		2	
p			$p>0.1$		$p>0.1$		$p<0.005$	

(continued)

Table 24, continued

# Years Used	Leeward Pure Spruce		Leeward Mixed Fir		Leeward Mixed Pine		Leeward Mixed Total		Total	
	f	$\hat{f}$	f	$\hat{f}$	f	$\hat{f}$	f	$\hat{f}$	f	$\hat{f}$
0	13	16.3	44	44.8	76	71.5	121	117.1	694	691.9
1	22	17.9	19	18.0	13	20.3	32	38.8	321	318.3
2	10	9.9	4	3.6	4	2.9	8	6.4	62	73.2
3	4	3.6			2	0.3	2	0.7	17	11.2
4									2	1.3
n	49		67		95		163		1096	
$\bar{X}$	1.102		0.403		0.284		0.331		0.460	
G	4.124[2]		[1]		[1]		2.532[2]		5.031[2]	
df	1						1		2	
p	$p>0.1$						$p>0.1$		$p>0.05$	

[1]This G-test was not performed because at least one class had an expected value less than 5 and lumping this class with the adjacent class would leave zero degrees of freedom.

[2]The two least frequent classes have been combined to calculate this statistic, so that the expected frequency would exceed five (Sokal and Rohlf 1969).

Table 25. The frequency of repeated use of individual trees on the Skelton study area. The log likelihood ratio tests (G) are based on a comparison between the observed frequencies (f) and the expected frequencies ($\hat{f}$) of a similar population (i.e. identical mean) with a Poisson distribution. The degrees of freedom associated with this goodness of fit test are the number of classes - 2 (Sokal and Rohlf 1969), so that this test is inappropriate for less than three classes.

# Years Used	Windward Fir f	Windward Fir $\hat{f}$	Windward Pine f	Windward Pine $\hat{f}$	Windward Total f	Windward Total $\hat{f}$	Leeward Pure Fir f	Leeward Pure Fir $\hat{f}$	Total f	Total $\hat{f}$
0	217	218.2	105	105.3	322	319.2	909	881.5	1231	1198.2
1	32	33.2	8	7.5	30	35.8	238	286.5	278	336.7
2	5	2.5			5	2.0	63	46.6	68	47.3
3							9	5.0	9	4.4
4							0	0.4	0	0.3
5							1	0.0	1	0.0
n	244		113		357		1220		1587	
$\bar{X}$	0.152		0.071		0.112		0.325		0.281	
G	[1]				[1]		17.766		22.912[2]	
df							2		1	
p							$p<0.005$		$p<0.005$	

[1]This G-test was not performed because at least one class had an expected value less than 5 and lumping this class with the adjacent class would leave zero degrees of freedom.

[2]The four least frequent classes have been combined to calculate this statistic, so that the expected frequency would exceed five.

more years than trees in high density stands (Table 26: Zoratti $G=10.608$ $p<0.001$; Skelton $G=16.360$ $p<0.001$ $df=1$), suggesting that the preferred type of tree was uncommon relative to the number of porcupines. Because of this relative scarcity, desirable Douglas fir on the Skelton area had a high probability of being used during several years (Table 25) and trees in low density stands were used, during at least one year, more frequently than trees in high density stands ($G=104.676$ $p<0.001$ $df=1$). On the Zoratti area however, the number of resident porcupines was apparently so great, during many winters, that trees in high and low density stands were used, at least once, in equivalent proportions ($G=2.8981$ $p>0.05$ $df=1$). If used trees in high density stands on the Zoratti area were of "poor quality", the probability of their being used during a subsequent winter would have been lower than for "good quality" trees, resulting in more trees than expected being used only once (Table 24).

Porcupine Feeding and Stand Density

The demonstrated correlation between stand density and the proportion of trees used by porcupines (Table 17) and the relationship between age and the intensity of use (Figure 12b) suggest two possible patterns of forest utilization. When the forest was relatively young and frequented by a limited number of porcupines, low density (preferred) stands should have received the most attention.

Table 26. A comparison of the frequency of porcupine feeding in high and low density plots. The numbers in parentheses are row percentages.

Zoratti

Density (#trees/100 sq. m)	Number of Years Used: 0	1	>1
<11.00	127 (48.7)	95 (36.4)	39 (14.9)
>11.00	75 (40.1)	99 (52.9)	13 (7.0)

Skelton

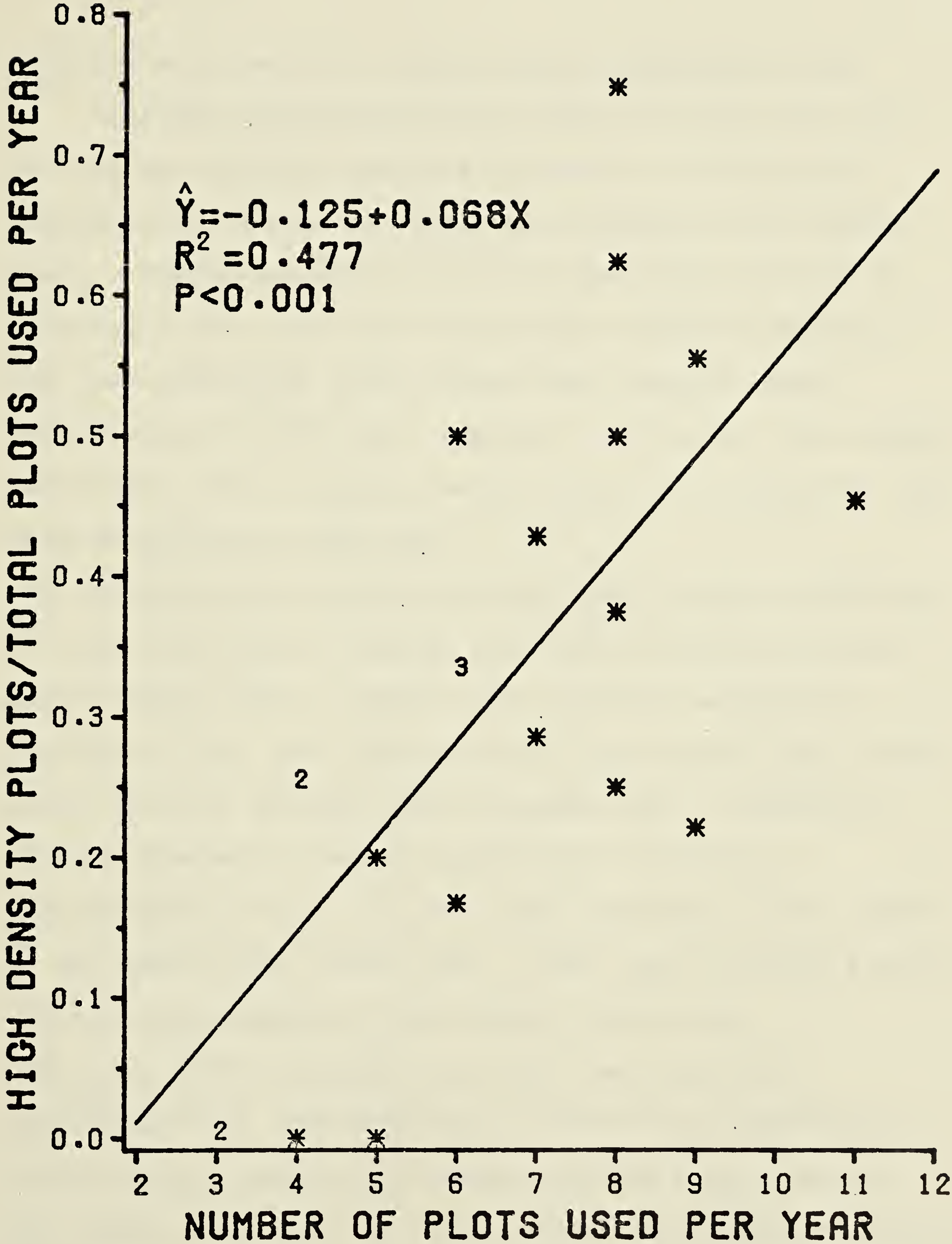
Density (#trees/100 sq. m)	Number of Years Used: 0	1	>1
<11.00	206 (54.2)	119 (31.3)	55 (14.5)
>11.00	703 (82.8)	128 (15.1)	18 (2.1)

As the forest grew and porcupine numbers increased, the porcupines could have crowded into the preferred type of stand, or some animals could have moved into the less preferred stands (see Fretwell 1972).

Whereas porcupines on the Zoratti area used a similar proportion of trees in high and low density plots (see Table 14: $G=1.586$ $p>0.1$ $df=1$), porcupines on the Skelton area showed a preference for trees in low density leeward plots (see Table 14: $G=93.130$ $p<0.001$ $df=1$). During the 32 year period from 1942 to 1974, an average ($\pm$ se) of 29.9 $\pm$ 3.78 percent of the leeward pure plots on the Zoratti area were used per year, while on the Skelton area during a similar period (1940-1972), 17.0 $\pm$ 1.78 percent of the leeward plots were used ($t=2.968$ $0.01>p>0.001$ S $df=44$). The high intensity of use experienced on the Zoratti area may not have allowed the expression of a preference for stands with less than 11 trees/100 sq. m.

Figure 13 illustrates an increase in the use of high density plots with increasing porcupine numbers on the Skelton area and provides additional evidence that high density stands are poorer quality porcupine habitat. (Only the period from 1949 to 1970 (see Figure 12a) was considered because the chance use of a high density plot when the population was small would have a much greater effect on the proportion of used plots that were high density than during population peaks.) In addition, this observation suggests that individual porcupines were aware of the distribution of

Figure 13. The relationship between the number of porcupines feeding in the Skelton leeward forest, as measured by the number of plots used per year, and the use of high density stands.


$\hat{Y}$=-0.125+0.068X
R^2 =0.477
P<0.001
HIGH DENSITY PLOTS/TOTAL PLOTS USED PER YEAR
NUMBER OF PLOTS USED PER YEAR
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
2
3
4
5
6
7
8
9
10
11
12

other porcupines around them, even though they are generally solitary animals (Taylor 1935; Curtis and Kozicky 1944).

Location and Amount of Feeding Within Individual Trees

Although porcupines feed on both the inner bark and foliage of conifers, evidence of feeding on foliage is ephemeral and cannot be adequately assessed after several years. Porcupines tend to feed in the upper portions of conifers on both the bole and lateral branches (Tables 27 and 28a: Gabrielson 1928; Taylor 1935; Shapiro 1949). Feeding scars on the upper surfaces of branches were usually encountered over a greater height range in a particular tree than were scars on the bole.

Usually less than 650 sq. cm of bark were removed from an individual tree, although many trees suffered greater damage (Table 28b). Feeding most commonly occurred on portions of the tree unprotected by corky bark, such as the distal ends of branches and the upper bole. Porcupines often succeeded in removing bark from the entire circumference of the bole of a tree resulting in the death of the upper crown (Table 28c). This type of damage has the greatest consequence on tree vigour (Storm and Halvorson 1967) and often can alter the form of an individual tree, particularly if the tree is regirdled in later years. Trees in low density stands in the leeward pure forest often had more bark removed by porcupines during single winters than trees in high density stands (Zoratti

Table 27. The average (± standard deviation) position of porcupine feeding within trees on the Zoratti and Skelton areas. Except for the column on the extreme right, position is measured on a scale on which ground level has a value of zero and the top of the tree has a value of one. Calculation of the position of the mode within the feeding range involved a similar scale on which the bottom and top of the feeding range within a tree had values of zero and one, respectively.

	Top of Feeding Range	Bottom of Feeding Range	Mode of Feeding Within Tree	Mode of Feeding Within Feeding Range
ZWF[1]	0.51±0.204 (11)[2]	0.29±0.212 (11)	0.38±0.207 (9)	0.62±0.243 (9)
ZPF	0.80±0.200 (233)	0.37±0.203 (233)	0.65±0.190 (121)	0.59±0.181 (165)
ZMF	0.58±0.275 (244)	0.24±0.170 (24)	0.40±0.214 (16)	0.60±0.164 (13)
ZPS	0.78±0.131 (43)	0.29±0.130 (43)	0.53±0.111 (16)	0.59±0.148 (18)
ZWP	0.63±0.275 (49)	0.33±0.242 (49)	0.51±0.237 (40)	0.57±0.242 (40)
ZMP	0.66±0.249 (16)	0.42±0.199 (16)	0.57±0.109 (7)	0.53±0.182 (12)
SWF	0.78±0.176 (19)	0.37±0.199 (19)	0.67±0.171 (10)	0.72±0.171 (19)
SPF	0.82±0.197 (179)	0.49±0.222 (179)	0.66±0.180 (78)	0.59±0.244 (182)
SWP	---- (2)	---- (2)	---- (2)	0.67±0.313 (6)

[1]Explanation of this comparison code is provided in Table 9.
[2]Sample size.

[illegible]

Table 28. Some characteristics of porcupine feeding in individual trees on the Zoratti and Skelton areas. Each entry indicates the number of trees in the respective class. Part a) is based upon trees that were used during a single year only.

	a) Branch Use Greater	Equal	Bole Use Greater	b) Area of Bark Removed per Year of Feeding (sq. cm) <650	650-1900	1900-3200	>3200	c) Frequency of Girdling per Tree[1] 0	1	2	3
ZWF	5	0	5	12	0	0	0				
ZPF	96	5	116	160	139	11	2				
ZMF	12	2	7	16	11	0	0				
ZPS	29	1	4	24	27	3	0				
ZWP	19	1	38	52	16	3	0				
ZMP	3	1	13	15	7	1	0				
SWF	25	3	8	38	4	0	0	29	8	0	0
SPF	208	5	77	299	85	9	2	172	105	30	4
SWP	1	0	3	6	2	0	0	6	3	0	0

[1] Appropriate data were not collected from the Zoratti area.

$G=22.872$ $p<0.001$ $df=2$: Skelton $G=18.942$ $p<0.001$ $df=2$).

The porcupines on the Zoratti and Skelton areas appear to have fed on the portions of trees in which food was most easily attainable and probably most nutritious. The phloem and foliage of conifers must supply much of the nutrients required for spring growth and therefore contain the highest concentrations of fats and carbohydrates of the aerial tissues (see Kramer and Kozlowski 1960 for a review). Tree growth is annually initiated at the bud bases and nutrients are drawn from the adjacent tissues (Kozlowski and Keller 1966) so that the bark and branches within the crown are important storage structures. The tendency of porcupines to feed on foliage from young branches (Taylor 1935; Curtis 1941; Shapiro 1949) and inner bark within the tree crown probably resulted in the consumption of the most nutritious food available.

CONCLUDING DISCUSSION

Preferences and Selection

Whether porcupines actually selected their food and habitat in the Zoratti and Skelton forests or merely relied upon chance, is central to understanding the patterns of forest use which have been observed. The disproportionate utilization of a specific segment of a resource relative to its occurrence in the environment has been regarded as a preference throughout the preceding discussion. Selection, the active expression of preferences involving discrimination between alternatives, is commonly inferred from a demonstration of preferences, often erroneously (Wiens 1976). The apparent relationship between the location of a forest and the intensity of its utilization by porcupines is a germane example of the occurrence of preferences without the involvement of selection.

Changes in the preferences of porcupines in relation to the number of individuals using an area intimate selection. The increased feeding in high density stands on the Skelton area when porcupines were relatively numerous (Figure 13) implies that these stands were accessible and usable, but probably not as desirable as low density stands. Deviation from randomness in the repeated use of individual trees in the leeward pure forests on both study areas, even though feeding in trees in other communities was a random event (Tables 24 and 25), is also suggestive of selective

behaviour. These observed preferences were seemingly mediated by the porcupines themselves, indicating an ability on their part to detect differences in quality.

Consumers cannot afford to be selective when resources are limited (Emlen 1966, 1968) and the presence of selection-based preferences therefore implies a relative abundance of food and habitat. Relaxation of selectivity was probably necessary on the more extensively used Zoratti area resulting in the apparent preference for smaller trees than were used on the Skelton area. The characteristics of the trees used by porcupines on the Skelton area may consequently be a better reflection of the physical qualities considered by porcupines in selecting trees.

Food Habits and Habitat Selection

Winter food and habitat selection by porcupines are apparently strongly interdependent. If a patch of bark or a branch of foliage are considered the food items of a porcupine feeding within a tree, the tree itself assumes the characteristics of a repeatable but uneven microhabitat throughout which the food items are scattered. Each individual tree supports many potential food items, although some are probably nutritionally or energetically satisfactory but unattainable because of their position. A porcupine that is foraging efficiently should therefore select trees on the probability of obtaining a relatively large quantity of suitable food items (Royama 1970;

MacArthur 1972).

This type of selection would require the presence of characters, such as bole diameter or crown width, which could be used to reliably distinguish profitable trees, preferably without unnecessarily expending energy in climbing. Chemical characteristics may be of little assistance in the selection of trees from ground level, because the living tissues at the base of a tree are often protected by several centimeters of corky bark which could hinder assessment of the present nutrient quality of the tree. With the exception of indications of porcupines feeding at ground level on limber pine in windward communities (see also Gill and Cordes 1972), basal scars were infrequently encountered during this study.

In addition to food, habitat must provide protection from predators and the elements. Rock dens supply these requirements when they are available to porcupines (Curtis 1941; Shapiro 1949), but in their absence, trees, thickets of brush, and windfalls serve as shelter (Taylor 1935; Curtis and Wilson 1953). Because neither study area offered suitable rock dens, individual trees must have furnished both food and shelter for the resident porcupines.

The selection of individual trees by porcupines could have occurred by two alternate procedures. A porcupine could seek out the appropriate community and, having found it, search for a suitable stand and finally decide upon an

attractive tree; or the entire selection process could involve only the search for an acceptable tree. Although either method of selection could have resulted in the observed preferences because large, vigorous, open-grown trees were most abundant in low density stands in the leeward pure forests, the occurrence of inter-community preferences and the absence of interspecific preferences suggest porcupines use the more efficient procedure of examining successively smaller units.

The strategy of food selection adopted by a particular individual or species is determined by the interaction of various constraints imposed by time, energy and nutrient requirements (Ellis et al. 1976). Porcupines are probably not confronted with a need to minimize the time spent feeding during the winter because they enjoy protection from most predators while situated in trees (Taylor 1935) and they are not involved in other time consuming activities. In addition, satisfaction of energy requirements is presumably not difficult for porcupines because these animals are often inactive for long periods during the winter (Taylor 1935; Brander 1973) and they can withstand moderately cold temperatures without dramatically elevating their metabolic rate (Irving et al. 1955: Winter lower critical temperature of Alaskan porcupines was -12° C). The fulfillment of nutrient requirements, particularly in forests that offer a limited number of food species, may therefore be the most influential factor in determining the

selection of winter food by porcupines.

Food value is the ultimate determinant of selection behaviour, even if the characters considered during the selection process are only correlated with a food's nutritive qualities (Fretwell 1972). The quality of a food item is a complex property which involves not only its nutrient content, but also the digestion and assimilation efficiency characteristics of the consuming individual (Longhurst et al. 1968) which are subject to the influence of secondary plant compounds (Freeland and Janzen 1974). In addition, an animal's response to a particular stimulus, such as a food with a specific nutrient content, can be greatly modified by its physiological state (Cabanac 1971). An awareness by porcupines of chemical qualities is not an assumption required to explain the observed porcupine preferences of communities, stands or individual trees, because vigorous trees can be identified by obvious physical features. Chemical attributes may, however, be more important within individual trees because porcupines appear to select food items through olfaction (Murie 1926; Taylor 1935).

Changes in food quality associated with ageing of the forests (see Cowan et al. 1950) have been suggested as a cause of the decline in use of the Zoratti and Skelton areas by porcupines. Temporal variability in food quality places a premium on dispersal behaviour because dispersal allows the occupation of habitats that have recently become

favourable (Wiens 1976). Porcupines are particularly mobile during the spring and fall when the availability of herbaceous food changes (Gabrielson and Horn 1930; Taylor 1935; Curtis and Wilson 1953) so that contact with new habitats could be frequent. Whether the declines in utilization of the Zoratti and Skelton areas were accompanied by a concurrent increase in the use of adjacent forests is difficult to assess. Fifteen to 20 forests within 30 kilometers of these study areas were superficially examined for indications of recent porcupine activity, without success. These forests were all approximately the same age, probably because of widespread fires (Dawson 1886), so that the general quality of coniferous forests that porcupines use as winter habitat in this region could be steadily declining.

Porcupines and Foraging Theory

There exists in the ecological literature a large body of information devoted to the optimal use of food and habitat (see Ellis *et al*. 1976 and Wiens 1976 for reviews). Although the theories proposed by individual studies often include components which are specific to a limited type of consumer (eg. Schoener 1969; Krebs *et al*. 1974; Pulliam 1974), basic precepts are apparent and they form the following allegorical summary of the observed dynamics of forest utilization by porcupines.

Animals foraging optimally should specialize when confronted by a relatively predictable abundance of food (Emlen 1966, 1968). On a short-term basis, this specialization is best accomplished through increased selectivity. Abundant food often results in a numerical response on the part of the consumer (Holling 1961), whether through immigration or increased success in reproduction, and an increase in consumer density. Continued exploitation of the food supply and an increase in the frequency of behavioural interactions with other consumers concurrent with this increase in density (Holling 1961) consequently reduce the relative suitability of the habitat. As this decline in suitability continues, the consumers must become less selective and begin using previously less attractive foods and habitat (Fretwell 1972). The increased use of different habitat types is accompanied by a change in the distribution of consumers from aggregation through randomness to uniformity (Grant and Morris 1971). A decline in the overall quality of the habitat, because of over-exploitation or intrinsic factors, should be accompanied by a decline in consumer density.

LITERATURE CITED

Assmann, E. 1970. The principles of forest yield study. Pergamon Press. Oxford. 506 pp.

Austin, M. P. 1971. Role of regression analysis in plant ecology. Proc. Ecol. Soc. of Australia 6:63-75.

Bannan, M. W. 1955. The vascular cambium and radial growth in Thuja occidentalis L. Can. J. Bot. 33:113-138.

Bates, C. G. 1923. Physiological requirements of Rocky Mountain trees. J. Agr. Res. 24:97-164.

Beaty, C. B. 1975. The landscapes of southern Alberta. Univ. of Lethbridge Prod. Serv. 95 pp.

Billings, W. D. 1952. The environmental complex in relation to plant growth and distribution. Q. Rev. Biol. 27:251-265.

Box, G. E. P. 1966. Use and abuse of regression. Technometrics 8:625-629.

Brander, R. B. 1973. Life-history notes on the porcupine in a hardwood-hemlock forest in upper Michigan. Mich. Acad. 5:425-433.

Brown, C. L. 1971a. Primary growth. Pages 1-66 In M. H. Zimmermann and C. L. Brown. Trees - Structure and Function. Springer-Verlag. New York. 336 pp.

____________. 1971b. Secondary growth. Pages 67-123 In M. H. Zimmermann and C. L. Brown. Trees - Structure and Function. Springer-Verlag. New York. 336 pp.

____________. 1971c. Growth and form. Pages 125-167 In M. H. Zimmermann and C. L. Brown. Trees - Structure and Function. Springer-Verlag. New York. 336 pp.

Cabanac, M. 1971. Physiological role of pleasure. Science 173:1103-1107.

Cormack, R. G. H. 1953. A survey of coniferous forest succession in the eastern Rockies. Forestry Chron. 29:218-232.

Cowan, I. M., W. S. Hoar and T. Hatter. 1950. The effect of forest succession upon the quantity and upon the nutritive values of woody plants used as food by moose. Can. J. Res. 28(D):249-271.

Crouch, G. L. 1969. Animal damage to conifers on National Forests in the Pacific Northwest Region. U.S.D.A. Forest Serv. Res. Bull. PNW-28. 13 pp.

Curtis, J. D. 1941. The silvicultural significance of the porcupine. J. Forestry 39:583-594.

Curtis, J. D. and E. L. Kozicky. 1944. Observations on the eastern porcupine. J. Mammal. 25:137-146.

Curtis, J. D. and A. K. Wilson. 1953. Porcupine feeding on Ponderosa pine in central Idaho. J. Forestry 51:339-341.

Daubenmire, R. F. 1943. Soil temperature versus drought as a factor determining the lower altitudinal limits of the trees in the Rocky Mountains. Bot. Gaz. 105:1-13.

________________. 1974. Taxonomic and ecologic relationships between _Picea glauca_ and _Picea engelmannii_. Can. J. Bot. 52:1545-1560.

Dawson, G. M. 1886. Preliminary report on the physical and geological features of that portion of the Rocky Mountains between latitude 49° and 51°30'. Geol. and Nat. Hist. Surv. of Canada Rep. 1B:1B-169B.

Dodge, W. E. 1967. The biology and life history of the porcupine in western Massachusetts. Ph.D. Thesis, Univ. Mass. 162 pp.

Draper, N. R. and H. Smith. 1966. Applied regression analysis. John Wiley. New York. 407 pp.

Eadie, J. 1970. Sheep production and pastoral resources. Pages 7-24 In A. Watson, (ed.) Animal populations in relation to their food resources. Blackwell. Oxford. 477 pp.

Ellis, J. E., J. A. Wiens, C. F. Rodell and J. C. Anway. 1976. A conceptual model of diet selection as an ecosystem process. J. Theor. Biol. 60:93-108.

Emlen, J. M. 1966. The role of time and energy in food preference. Amer. Natur. 10:611-0617.

___________. 1968. Optimal choice in animals. Amer. Natur. 102:385-389.

Forestry Handbook for British Columbia. 1971. Univ. of British Columbia Forest Club. Vancouver. Third edition. 815 pp.

Freeland, W. J. and D. H. Janzen. 1974. Strategies in herbivory by mammals: the role of plant secondary compounds. Amer. Natur. 108:269-289.

Fretwell, S. D. 1972. Populations in a seasonal environment. Monogr. Pop. Biol. 5. Princeton Univ. Press. 217 pp.

Gabrielson, I. N. 1928. Notes on the habits and behavior of the porcupine in Oregon. J. Mammal. 9:33-38.

Gabrielson, I. N. and E. E. Horn. 1930. Porcupine control in the western states. U.S.D.A. Leaflet No. 60. 8 pp.

Gill, D. and L. D. Cordes. 1972. Winter habitat preference of porcupines in the southern Alberta foothills. Can. Field-Nat. 86:349-355.

Grant, P. R. and R. D. Morris. 1971. The distribution of Microtus pennsylvanicus within grassland habitat. Can. J.Zool. 49:1043-1052.

Grillos, S. J. and F. H. Smith. 1959. The secondary phloem of Douglas-fir. Forest Sci. 5:377-388.

Holling, C. S. 1961. Principles of insect predation. Ann. Rev. Entomol. 6:163-182.

Husch, B. 1963. Forest mensuration and statistics. Ronald. New York. 474 pp.

Husch, B., C. I. Miller and T. W. Beers. 1972. Forest mensuration. Ronald. New York, Second edition. 410 pp.

Irving, L., H. Krog and M. Monson. 1955. The metabolism of some Alaskan animals in winter and summer. Physiol. Zool. 28:173-185.

Jacobs, M. R. 1954. The effect of wind sway on the form and development of *Pinus radiata* D. Don. Australian J. Bot. 2:35-51.

Kim, J. and F. J. Kohout. 1975. Multiple regression analysis: subprogram regression. Pages 320-367 *In* N. H. Nie *et al*. Statistical Package for the Social Sciences. McGraw-Hill. New York, Second edition. 675 pp.

Klecka, W. R. 1975. Discriminant analysis. Pages 434-467 *In* N. H. Nie *et al*. Statistical Package for the Social Sciences. McGraw-Hill. New York, Second edition. 675 pp.

Kozlowski, T. T. and T. Keller. 1966. Food relations of woody plants. Bot. Rev. 32:293-382.

Kramer, P. J. and T. T. Kozlowski. 1960. The physiology of trees. McGraw-Hill. New York. 642 pp.

Krebs, J. C., J. C. Ryan and E. L. Charnov. 1974. Hunting by expectation or optimal foraging? A study of patch use by chickadees. Anim. Behav. 22:953-964.

Krefting, L. W., J. H. Stoeckeler, B. J. Bradle and W. D. Fitzwater. 1962. Porcupine-timber relationships in the Lake States. J. Forestry 60:325-330.

Longhurst, W. N., H. K. Oh, M. B. Jones and R. E. Kepner. 1968. A basis for the palatability of deer forage plants. 33rd. N. Am. Wildl. Natur. Resour. Conf. Trans. pp. 181-189.

Longley, R. M. 1972. The climate of the prairie provinces. Climatol. Stud. No. 13. Environment Canada. 79 pp.

MacArthur, R. H. 1972. Geographical ecology. Harper and Row. New York. 269 pp.

Marr, J. W. 1967. Ecosystems of the east slope of the Front Range in Colorado. Univ. Colorado Stud. Ser. in Biol. 8. 134 pp.

McGinnies, W. G. 1963. Dendrochronology. J. Forestry 61:5-11.

McMinn, R. G. 1952. The role of soil drought in the distribution of vegetation in the northern Rocky Mountains. Ecology 33:1-15.

Mitchell, K. J. 1969. Simulation of the growth of even aged stands of white spruce. Yale Univ. School of Forest. Bull. 75. 48 pp.

Morrison, D. G. 1974. Discriminant analysis. Pages 2.442-2.457 In R. Ferber. Handbook of Marketing Research. McGraw-Hill. New York.

Moss, E. H. 1944. The prairie and associated vegetation of southwestern Alberta. Can. J. Res. 22(C):11-31.

Moss, E. H. and J. A. Campbell. 1947. The fescue grassland of Alberta. Can. J. Res. 25(C):209-227.

Murie, O. J. 1926. The porcupine in northern Alaska. J. Mammal. 7:109-113.

Nie, N. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner and D. H. Bent. 1975. Statistical Package for the Social Sciences. McGraw-Hill. New York, Second edition. 675 pp.

Pearson, G. A. 1920. Factors controlling the distribution of forest types, Part II. Ecology 1:289-308.

Poole, R. W. 1974. An introduction to quantitative ecology. McGraw-Hill. New York. 532 pp.

Pulliam, H. R. 1974. On the theory of optimal diets. Amer. Natur. 108:59-74.

Reukema, D. L. 1959. Missing annual rings in branches of young-growth Douglas-fir. Ecology 40:480-482.

Rowe, J. S. 1972. Forest regions of Canada. Dept. of the Environment. Can. Forest. Serv. Publ. No. 1300. 172 pp.

Royama, T. 1970. Factors governing the hunting behaviour and selection of food by the great tit (*Parus major* L.). J. Animal Ecol. 39:619-668.

Rudolf, P. O. 1949. Porcupines' preferences in pine plantations. J. Forestry 47:207-209.

Schoener, T. W. 1969. Optimal size and specialization in constant and fluctuating environments: An energy-time approach. Brookhaven Symp. Biol. 22:103-114.

Schulman, E. 1956. Dendroclimatic changes in semiarid America. Univ. Ariz. Press. Tucson. 142 pp.

Shapiro, J. 1949. Ecological and life history notes on the porcupine in the Adirondacks. J. Mammal. 30:247-257.

Sokal, R. R. and F. J. Rohlf. 1969. Biometry. W. H. Freeman. San Francisco. 776 pp.

Spencer, D. A. 1964. Porcupine population fluctuations in past centuries revealed by dendrochronology. J. Appl. Ecol. 1:127-149.

Steel, R. G. D. and J. H. Torrie. 1960. Principles and procedures of statistics. McGraw-Hill. New York. 481 pp.

Storm, G. L. and C. H. Halvorson. 1967. Effect of injury by porcupines on radial growth of Ponderosa pine. J. Forestry 65:740-743.

Tatsuoka, M. M. 1969. Validation studies. The use of multiple regression equations. Inst. for Personality and Ability Testing. Champaign Ill. 28 pp.

______________. 1970. Discriminant analysis - The study of group differences. Inst. for Personality and Ability Testing. Champaign Ill. 57 pp.

Taylor, W. P. 1935. Ecology and life history of the porcupine (Erethizon epixanthum) as related to the forests of Arizona and southwestern United States. Univ. Ariz. Bull. 6:1-177.

van Deusen, J. L. and C. A. Myers. 1962. Porcupine damage in immature stands of ponderosa pine in the Black Hills. J. Forestry 60:811-813.

Wiens, J. A. 1976. Population responses to patchy environments. Ann. Rev. Ecol. and Syst. 7:81-120.

Wyatt, F. A., W. E. Bowser and W. Odynsky. 1939. Soil survey of the Lethbridge and Pincher Creek Sheets. Univ. Alta. Coll. of Agr. Bull. No. 32. 98 pp.

Appendix 1. Error in the Calculation of Past Diameters.

The calculation of past diameters is based upon the equation,

$$IRx=(a+(b \bullet DBH)) \bullet [(TC-\sum_{n=1}^{n=x} In)/TC] \qquad (1)$$

in which: x represents the number of years prior to the measurement of the diameter at breast height (DBH); IR represents the radius inside the bark at time x; TC represents the total length of the increment core at breast height; I represents the size of the annual increment accrued during year n; and a and b are the constants from a linear regression equation relating the measured DBH and inside radius. All quantities on the right of this equation were measured directly, with the exception of TC which is a derived variable (see Methods). Since increment cores were extracted at stump height, the core length can be subdivided into the equivalent core length at breast height (TC) and the core length differential (CD) which represents diameter growth before the tree reached breast height. The age at breast height (ABH) has been calculated using regression techniques (see Methods) and the measured size of the growth increment corresponding to this age represents CD. Error in calculating past diameters is therefore primarily associated with the estimate of ABH and perpetuated through the measurement of CD and the calculation of TC.

The following examples are an examination of the magnitude of the error involved in determining the past

diameters of cored trees and the relationship of this error to tree age and stand density. Three Douglas fir trees from the Zoratti leeward pure association have been used in this demonstration. Tree 2304 is from a low density plot while 3727 and 3749 are from the same high density plot. In addition to the calculated value of TC, two values are provided which represent ± 0.5 cm errors in the estimation of CD.

Since TC contributes to both the numerator and the denominator of the quantity within the square brackets in equation (1), any error involved in calculating CD tends to cancel itself out and the influence of a relatively large error in the value of TC on the overall calculation of past diameters is therefore slight. The effect of an overestimate is generally greater than that of an underestimate. In addition, the size of the error is inversely related to both the age of the tree and stand density, but directly related to the number of years prior to measurement of the tree for which a diameter is desired. Although no conclusive evidence is available it is proposed that the mean error associated with the past diameters at breast height does not exceed five percent and that this error does not significantly affect the conclusions regarding the size and form of trees used by porcupines.

Tree 2304

DBH=28.9 cm
Bark=1.02 cm
Age=69 yr
Core=13.22 cm

Age at Breast Height=20 yr
Core Differential=3.350 cm

Density=7.77 trees/100 sq. m

TC=13.22-3.350		
=9.87 cm	10.37 cm	9.37 cm
IR =(-0.160+(0.456•28.9))•((9.87-0.776)/9.87)		
=12.0 cm	12.04 cm	11.94 cm
DBH =26.6 cm	27.7 cm	26.5 cm
% Error	0.36	0.38
IR =(-0.160+(0.456•28.9))•((9.87-2.228)/9.87)		
=10.08 cm	10.22 cm	9.92 cm
DBH =22.4 cm	22.7 cm	22.1 cm
% Error	1.32	1.36
IR =(-0.160+(0.456•28.9))•(9.87-4.263)/9.87)		
=7.40 cm	7.67 cm	7.10 cm
DBH =16.6 cm	17.2 cm	15.9 cm
% Error	3.49	4.40

Tree 3727

DBH=13.3 cm	Age at Breast Height=20 yr
Bark=0.76 cm	Core Differential=2.735 cm
Age=73 yr	
Core=5.32 cm	Density=18.66 trees/100 sq. m

TC=5.32-2.735		
=2.59 cm	3.09 cm	2.09 cm
IR =(-0.160+(0.456•13.3))•((2.59-0.083)/2.59)		
=5.71 cm	5.74 cm	5.67 cm
DBH =12.9 cm	12.9 cm	12.8 cm
% Error	0	0.78
IR =(-0.160+(0.456•13.3))•((2.59-0.165)/2.59)		
=5.52 cm	5.58 cm	5.43 cm
DBH =12.5 cm	12.6 cm	12.3 cm
% Error	0.79	1.63
IR =(-0.160+(0.456•13.3))•((2.59-0.418)/2.59)		
=4.95 cm	5.10 cm	4.72 cm
DBH =11.2 cm	11.5 cm	10.7 cm
% Error	2.61	4.67

Tree 3749

DBH=7.3 cm
Bark=0.53 cm
Age=49 yr
Core=3.14 cm

Age at Breast Height=20 yr
Core Differential=1.456 cm

Density=18.66 trees/100 sq. m

TC=3.14-1.465		
=1.68 cm	2.18 cm	1.18 cm
IR =(-0.160+(0.456•7.3))•((1.68-0.110)/1.68)		
=2.95 cm	3.00 cm	2.86 cm
DBH =6.8 cm	6.9 cm	6.7 cm
% Error	1.45	1.49
IR =(-0.160+(0.456•7.3))•((1.68-0.187)/1.68)		
=2.81 cm	2.89 cm	2.66 cm
DBH =6.5 cm	6.7 cm	6.2 cm
% Error	2.99	4.84
IR =(-0.160+(0.456•7.3))•((1.68-0.253)/1.68)		
=2.68 cm	2.79 cm	2.48 cm
DBH =6.3 cm	6.5 cm	5.8 cm
% Error	3.08	8.62

Appendix 2. Multivariate Statistical Techniques

Multiple Regression

Multiple regression is a statistical technique designed to examine the extent of mathematical dependence of a particular variable (dependent or criterion variable; Y) on a set of associated variables (independent or predictor variables; $X_1 \ldots X_n$). The outcome of an analysis of this type is an equation of the form

$$\hat{Y}=a+b_1 X_1+b_2 X_2+\ldots b_n X_n$$

where $\hat{Y}$ is the predicted value of the dependent variable under the specified conditions of the independent variables, X_1 through X_n and a and $b_1 \ldots b_n$ are constants derived by the procedure of least squares. This equation is asymmetrical in the sense that although changes in the magnitude of the independent variables can be expected to elicit changes in the dependent variable, the reverse is not true.

The data must conform with a series of assumptions to be suitable for multiple regression analysis (Poole 1974). The dependent variable must be normally distributed and the relationships between it and the independent variables must be linear and additive. Although multiple regression is quite robust, extreme correlations between the independent variables can affect the results. Finally, the differences between the observed and predicted values of the dependent variables (residuals) must be normally distributed with a mean of zero and a constant variance.

Since regression analysis is associated with an esoterica that often obscures its usefulness, a list of more commonly encountered terms is provided. The general form of the multiple regression equation given above contained two types of constants:

a - represents the predicted value of the dependent variable when the values of all the independent variables are zero (Poole 1974).

$b_1 \ldots b_n$ - the partial regression coefficients represent the magnitude and direction of change in the dependent variable when the associated independent variable is increased by one unit and there is no change in the size of the other independent variables. If these coefficients are calculated from standardized data (transformed to have a mean of zero and a standard deviation of one, the unit of measure being one standard deviation) they are known as beta weights (Draper and Smith 1966). Confidence in a partial regression coefficient is expressed in its standard error which describes the variability involved in sampling a particular population (Kim and Kohout 1975).

The usefulness of a calculated equation can be measured in several ways:

multiple correlation coefficient (R) - describes the mutual relationship between the observed value of the dependent variable and the value predicted from the prevailing values of the independent variables

(Tatsuoka 1969). The square of this value, R^2 (coefficient of multiple determination), represents the proportion of the total variation of the dependent variable explained by the calculated regression equation (Draper and Smith 1966).

standard error of the estimate - the dimension of one standard deviation for observed values of the dependent variable about the regression equation (Draper and Smith 1966).

overall F-test - a significance test that assesses the effectiveness of the regression equation to explain more variation in the dependent variable than would be expected if the equation were drawn at random (Draper and Smith 1966).

Although a particular equation offers a statistically significant explanation of the variation in the dependent variable, the importance of individual independent variables could be negligible. Examination of each partial regression coefficient by a partial F-test demonstrates the ability of the corresponding independent variable to explain variation in the dependent variable left unexplained by other variables in the equation.

Before attempting to calculate any regression equations the data were examined to ensure that all assumptions were satisfied. If, after conducting a Kolmogorov-Smirnov goodness of fit test, the dependent variable was found not to be normally distributed, a suitable transformation was

applied. Simple correlation coefficients were used as an index of a linear relationship between the dependent variable and five forms of each independent variable (untransformed, square, square root, log, inverse). The combination with the largest coefficient was selected for use in the analysis. Following selection of the "best" regression equation, the predicted values of the dependent variable were plotted against the actual values and these plots were visually examined for patterns that could expose violations of the assumptions regarding the distribution of residuals and the additivity requirement.

A forward selection procedure was used to derive regression equations that contained only those independent variables which were useful in explaining variation in the dependent variable. Independent variables were selected to enter the equation one at a time on the basis of their partial correlation coefficient. This coefficient describes the association between the dependent variable and a specific independent variable when the effects of the independent variables already in the equation are held constant. The process of adding independent variables with the highest partial coefficients continued until none of the remaining potential independent variables could explain a statistically significant amount of the remaining unexplained variation as determined by partial F-tests (Kim and Kohout 1975). Draper and Smith (1966) however suggest that the forward selection technique is not completely

adequate since a variable which entered the equation at an early stage may become superfluous because of its relationship with variables that entered the equation later. For this reason, each of the partial F-tests for all variables in the final equation were examined for significance. If the contribution of any variable had fallen below the acceptance level ($p \leq 0.05$) it was removed from the equation and the selection process was resumed.

Independent variables in the equation may be highly correlated with unmeasured variables which are in fact responsible for variation in the dependent variables (Box 1966). Because the occurrence of these "latent" variables is to be expected in the analysis of biological systems, Austin (1971) has stated that the success of a multiple regression equation is measured not only by the size of the coefficient of multiple determination, but also by the ability to provide a biological interpretation for the terms in the equation.

<u>Discriminant Analysis</u> (see Tatsuoka 1970 and Morrison 1974)

The objective of discriminant analysis is to devise a classification scheme that will best distinquish between several exclusive groups. This technique involves the derivation of a series of equations that can be used to calculate a score (Z_i) for each individual or object based on the values of a set of independent variables ($X_{1i} \ldots X_{ni}$) associated with it (Morrison 1974). These equations take the form

$$Z_i = a_i + b_{1i} X_{1i} + \ldots b_{ni} X_{ni}$$

in which a_i and $b_{1i} \ldots b_{ni}$ are constants analogous to the various regression coefficients. Unlike regression analysis however, the value of the discriminant score does not bear an exact, intuitive connotation; it is merely a classification scale. The probability of an individual with a given discriminant score belonging to one of the exclusive groups varies along this classification scale. By comparing each individual score with a critical value designating the probability boundary between two groups, each individual can be allotted to a group. Because discriminant functions are linear they may not adequately classify three or more groups and additional equations may be necessary. Discriminant analysis was used to distinquish only two groups in this study (used and unused trees) so that the complications involved in more detailed analysis are not considered here (consult Tatsuoka 1970).

Discriminant analysis can be used in two ways; classification and interpretation. Classification involves deriving a series of discriminant functions from known individuals and using them to categorize unknown individuals on the basis of associated independent variables. Interpretation, the use to which this technique was put in this study, involves determining which of the independent variables are most effective in grouping individuals. The ability of an independent variable to increase the power of a discriminant function is inversely measured by Wilks' lambda, which can be transformed into a chi-square statistic for significance testing (Klecka 1975). Using a stepwise procedure, those independent variables that make a significant contribution to the discriminant function can be identified.

Appendix 3. Detailed Multiple Regression Statistics

The statistics that follow are more extensive descriptions of the relationships between variables outlined in Tables 5, 6, 7, 17 and 23. The name of the dependent variable is found in the upper left corner of each block of statistics, followed by the test statistic (Z) and probability level for the Kolmogorov-Smirnov test for normality. The first column of numbers below this information includes the statistics for the overall regression equation: R^2 - the proportion of variation explained by the entire equation: se - the standard error of the estimate; F - the overall F-test; and cons. - the value of the Y-intercept. Columns to the right contain statistics particular to the respective independent variables: se - the standard error of the regression coefficient; F - the partial F-test; cons. - the regression coefficient; and beta - the standardized regression coefficient. Independent variables are listed from left to right in the order in which they entered the regression equation. The R^2 value associated with each independent variable is a measure of its contribution in explaining the variation that remained unexplained by the independent variables to its left. The numbers in braces refer to the type of transformation applied to a variable: {1} squared; {2} square root; {3} log; {4} inverse; {5} arcsin.

Zoratti Windward Fir Tables 5, 6 and 7

DBH {3} Z=0.481 p>0.9

		Age {4}
n	25	
R	0.740	
R^2	0.548	0.548
se	0.284	7.215
F	27.874	27.874
p	p<0.001	p<0.001
cons.	1.591	-38.094
beta		-0.740

Height {3} Z=0.460 p>0.9

		Age {4}
n	24	
R	0.632	
R^2	0.399	0.399
se	0.175	4.463
F	14.600	14.600
p	p<0.001	p<0.001
cons.	0.898	-17.054
beta		-0.632

CI Z=0.551 p>0.9

		Age {4}	Slope {4}
n	24		
R	0.757		
R^2	0.573	0.485	0.088
se	0.670	17.131	0.971
F	14.088	22.238	4.335
p	p<0.001	p<0.001	0.05>p>0.025
cons.	3.393	-80.734	2.022
beta		-0.674	0.298

Skelton Windward Fir Tables 5, 6 and 7

DBH {2} Z=0.359 p>0.9

		Age {4}	Exposure {1}	Density {4}
n	54			
R	0.736			
R^2	0.542	0.217	0.251	0.074
se	0.714	24.733	0.00001	2.221
F	19.695	35.592	31.509	8.084
p	p<0.001	p<0.001	p<0.001	0.01>p>0.005
cons.	2.769	-147.556	0.00004	6.316
beta		-0.583	0.553	0.276

Height {2} Z=0.786 p>0.5

		Exposure {1}	Age {2}
n	49		
R	0.552		
R^2	0.304	0.125	0.179
se	0.493	0.000	0.072
F	10.066	13.452	11.854
p	p<0.001	p<0.001	0.005>p>0.001
cons.	-0.729	0.00002	0.249
beta		0.467	0.438

CI {3} Z=0.638 p>0.75

		Density {1}	Age {4}
n	49		
R	0.510		
R^2	0.260	0.149	0.111
se	0.095	0.0002	3.641
F	8.067	10.732	6.901
p	0.005>p>0.001	0.005>p>0.001	0.025>p>0.01
cons.	0.580	-0.0006	-9.563
beta		-0.417	-0.335

Zoratti Leeward Pure Fir   Tables 5, 6 and 7

DBH {2}   Z=0.589   p>0.75

		Age {3}	Density
n	104		
R	0.796		
R^2	0.633	0.499	0.133
se	0.723	0.502	0.014
F	87.071	102.123	36.701
p	p<0.001	p<0.001	p<0.001
cons.	-3.974	5.072	-0.084
beta		0.624	-0.374

Height   Z=1.309   p>0.05

		Age {3}	Density
n	88		
R	0.772		
R^2	0.596	0.522	0.074
se	2.849	2.054	0.060
F	62.668	89.919	15.501
p	p<0.001	p<0.001	p<0.001
cons.	-21.228	19.474	-0.238
beta		0.667	-0.277

CI {2}   Z=0.606   p>0.75

		Age {4}	Density {3}
n	88		
R	0.515		
R^2	0.265	0.171	0.094
se	0.197	2.787	0.106
F	15.326	13.957	10.823
p	p<0.001	p<0.001	0.005>p>0.001
cons.	1.813	-10.411	-0.347
beta		-0.354	-0.312

Skelton Leeward Pure Fir   Tables 5, 6 and 7

DBH {2}   Z=0.566   p>0.9

		Age {3}	Density {4}
n	247		
R	0.755		
R^2	0.570	0.487	0.083
se	0.733	0.370	1.098
F	161.590	277.211	47.062
p	p<0.001	p<0.001	p<0.001
cons.	-7.525	6.168	7.534
beta		0.699	0.288

Height   Z=1.680   p=0.007 (not normally distributed)

		Age {3}	Exposure {4}
n	219		
R	0.698		
R^2	0.487	0.476	0.012
se	3.025	1.487	735.078
F	102.705	204.909	4.913
p	p<0.001	p<0.001	0.05>p>0.025
cons.	-21.765	21.289	-1629.386
beta		0.701	-0.109

CI {3}   Z=0.845   p>0.25

		Age {4}	Density {3}
n	219		
R	0.656		
R^2	0.431	0.293	0.138
se	0.116	1.015	0.040
F	81.723	120.538	52.340
p	p<0.001	p<0.001	p<0.001
cons.	0.679	-11.143	-0.288
beta		-0.565	-0.372

Zoratti Leeward Mixed Fir Tables 5, 6 and 7

DBH {3} Z=0.929 p>0.25

		Age {2}
n	28	
R	0.823	
R^2	0.677	0.677
se	0.271	0.032
F	54.537	54.537
p	p<0.001	p<0.001
cons.	-0.652	0.239
beta		0.832

Height {3} Z=0.660 p>0.75

		Age {3}
n	25	
R	0.792	
R^2	0.628	0.628
se	0.166	0.140
F	38.788	38.788
p	p<0.001	p<0.001
cons.	-0.695	0.874
beta		0.792

CI {2} Z=0.672 p>0.75

		Age
n	25	
R	0.829	
R^2	0.687	0.687
se	0.182	0.002
F	50.395	50.395
p	p<0.001	p<0.001
cons.	0.756	0.013
beta		0.829

Zoratti Windward Pine Tables 5, 6 and 7

DBH {2} Z=0.469 p>0.9

		Age {2}	Slope {4}
n	94		
R	0.685		
R^2	0.469	0.425	0.044
se	0.646	0.047	0.231
F	40.211	75.274	7.534
p	p<0.001	p<0.001	0.01>p>0.005
cons.	-0.711	0.412	0.634
beta		0.664	0.210

Height {3} Z=0.807 p>0.5

		Age {3}	Slope {4}
n	83		
R	0.597		
R^2	0.356	0.292	0.064
se	0.125	0.101	0.047
f	22.137	39.408	7.984
p	p<0.001	p<0.001	0.01>p>0.005
cons.	-0.728	0.636	0.133
beta		0.566	0.255

CI Z=0.960 p>0.25

		Age {2}	Slope {1}
n	83		
R	0.678		
R^2	0.459	0.420	0.039
se	0.730	0.056	0.0003
F	33.964	65.556	5.836
p	p<0.001	p<0.001	0.05>p>0.025
cons.	-0.842	0.450	-0.0008
beta		0.670	-0.200

Skelton Windward Pine Tables 5, 6 and 7

DBH {4} Z=1.044 p>0.1

		Age {4}
n	19	
R	0.652	
R^2	0.425	0.425
se	0.043	1.772
F	12.585	12.585
p	0.005>p>0.001	0.005>p>0.001
cons.	0.010	6.287
beta		0.652

Height {3} Z=0.803 p>0.5

		Exposure {1}
n	12	
R	0.720	
R^2	0.519	0.519
se	0.084	0.000
F	10.780	10.780
p	0.025>p>0.01	0.025>p>0.01
cons.	0.327	0.00004
beta		0.720

CI Z=0.498 p>0.9

		Density {4}
n	12	
R	0.585	
R^2	0.343	0.343
se	0.439	8.008
F	5.211	5.211
p	0.05>p>0.025	0.05>p>0.025
cons.	4.554	-18.280
beta		-0.585

Zoratti Leeward Mixed Pine Tables 5, 6 and 7

DBH Z=0.530 p>0.9

		Age
n	31	
R	0.678	
R^2	0.459	0.459
se	5.296	0.048
F	24.623	24.623
p	p<0.001	p<0.001
cons.	0.472	0.238
beta		0.678

Height {2} Z=0.711 p>0.5

		Age	Slope {1}
n	26		
R	0.742		
R^2	0.511	0.443	0.108
se	0.359	0.052	0.0004
F	14.099	27.831	5.538
p	p<0.001	p<0.001	0.05>p>0.025
cons.	0.932	0.274	-0.001
beta		0.878	-0.391

CI Z=0.465 p>0.9

		Age	Slope {1}	Density {4}
n	26			
R	0.804			
R^2	0.647	0.427	0.110	0.110
se	0.585	0.007	0.001	2.238
F	13.451	36.056	9.410	6.888
p	p<0.001	p<0.001	0.005>p>0.001	0.005>p>0.001
cons.	0.877	0.041	-0.002	5.874
beta		0.951	-0.490	0.338

Zoratti Windward Table 17

Proportion of Trees Used Z=0.297 p>0.9

		Density {4}
n	9	
R	0.744	
R^2	0.553	0.553
se	0.075	0.744
F	8.656	8.656
p	0.025>p>0.01	0.025>p>0.01
cons.	0.043	2.189
beta		0.744

Skelton Windward

Proportion of Trees Used Z=0.618 p>0.75

Not significant F=4.250 p>0.05

Zoratti Leeward Pure Table 17

Proportion of Trees Used {5} Z=0.264 p>0.9

		Density {1}	Slope {4}
n	12		
R	0.706		
R^2	0.499	0.185	0.314
se	9.011	12.950	549.894
F	4.482	8.222	5.633
p	0.05>p>0.025	0.025>p>0.01	0.05>p>0.025
cons.	129.933	-37.132	-1305.128
beta		-0.833	-0.690

Skelton Leeward Pure Table 17

Proportion of Trees Used Z=0.897 p>0.3

		Density {3}	Slope {3}	Exposure {1}
n	29			
R	0.847			
R^2	0.717	0.407	0.230	0.080
se	0.136	0.125	0.173	0.000
F	21.117	20.533	12.336	7.099
p	p<0.001	p<0.001	0.005>p>0.001	0.025>p>0.01
cons.	-0.286	-0.564	0.607	0.000003
beta		-0.500	0.396	0.307

Zoratti Leeward Mixed Table 17

Proportion of Trees Used Z=0.457 p>0.9

		Proportion of Douglas Fir
n	5	
R	0.958	
R^2	0.917	0.917
se	0.077	0.145
F	33.162	33.162
p	0.025>p>0.01	0.025>p>0.01
cons.	-0.001	0.835
beta		0.958

Zoratti Combined   Table 17

Proportion of Trees Used   Z=0.470   p>0.9

		#fir/#total	X DBH {2}
n	27		
R	0.844		
R^2	0.713	0.652	0.061
se	0.146	0.120	0.060
F	29.782	5.737	5.073
p	p<0.001	0.05>p>0.025	0.05>p>0.025
cons.	-0.193	0.287	0.135
beta		0.456	0.429

Skelton Combined   Table 17

Proportion of Trees Used   Z=1.170   p>0.1

		Exposure {1}	Density {4}	Slope {4}
n	40			
R	0.792			
R^2	0.628	0.348	0.237	0.043
se	0.151	0.000	0.480	0.916
F	20.238	17.387	23.422	4.196
p	p<0.001	p<0.001	p<0.001	0.05>p>0.025
cons.	-0.256	0.000003	2.322	-1.875
beta		0.479	0.492	-0.235

Zoratti Table 23

$\bar{X}$ DBH Z=0.597 p>0.75

		Use Age {3}
n	17	
R	0.831	
R^2	0.690	0.690
se	3.089	2.363
F	33.337	33.337
p	p<0.001	p<0.001
cons.	30.503	-13.644
beta		-0.831

$\bar{X}$ Height {1} Z=0.619 p>0.75

Not significant F=3.815 p>0.05

$\bar{X}$ CI {1} Z=0.758 p>0.5

		Use Age {4}
n	17	
R	0.841	
R^2	0.707	0.707
se	0.934	1.035
F	36.125	36.125
p	p<0.001	p<0.001
cons.	2.620	6.222
beta		0.941

Skelton Table 23

$\bar{X}$ DBH {1} Z=0.431 p>0.9

Not significant F=4.277 p>0.05

$\bar{X}$ Height {1} Z=0.602 p>0.75

Not significant F=1.446 p>0.1

$\bar{X}$ CI {4} Z=0.593 p>0.874

		Use Age {4}
n	16	
R	0.526	
R^2	0.277	0.277
se	0.050	0.0001
F	5.366	5.366
p	0.05>p>0.025	0.05>p>0.025
cons.	0.409	0.0003
beta		0.526